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MEMOIRS OF THE QUEENSLAND MUSEUM, VOLUME 32

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ANOPSILANA BARNARDI, A NEW SPECIES OF ESTUARINE CIROLANID CRUSTACEAN ISOPOD FROM TROPICAL EASTERN AUSTRALIA

NIEL L. BRUCE

Bruce, N.L. 1992 06 29: *Anopsilana barnardi*, a new species of estuarine cirolanid crustacean isopod from tropical eastern Australia. *Memoirs of the Queensland Museum* 32(1): 1-8. Brisbane. ISSN 0079-8835.

Anopsilana barnardi sp.nov., the third species of *Anopsilana* recorded from Australia, is described from northeastern Queensland. A key to the Australian species is given and a list of all *Anopsilana* species is provided.□ *Isopoda, Cirolanidae, new species, northeastern Queensland, Southwest Pacific, taxonomy.*

Niel L. Bruce, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 10 January, 1992.

Anopsilana Paulian & Deboutteville, 1956, contains thirteen species. Its occurrence is restricted to the tropical regions of the world; about half the species are recorded from troglobitic habits (both freshwater and euryhaline), the others are all recorded from mangrove or estuarine habitats.

Anopsilana barnardi sp.nov. was taken from a mid-stream grab sample in the Murray River, and it is therefore not directly associated with mangroves as are the other Australian species of *Anopsilana.*

Anopsilana Paulian & Deboutteville

Anopsilana Paulian & Deboutteville, 1956: 87. Bruce, 1981: 955, fig. 5i-e; 1986: 196; Kensley & Schotte, 1989: 124; Brusca, Wetzer & France (in press).

Troglocirolana Rioja, 1956: 447 [Type species: *Cirolana cubensis* Hay, 1903, by monotypy].

Haitilana Notenboom, 1981: 314 [Type species: *Haitilana radicicola* Notenboom, 1981, original designation].

Type Species

Anopsilana poissoni Paulian & Deboutteville, 1956, original designation. The location of the types was not given in the original publication, but was cited as at the Institute Scientific de Madagascar, Tsimbazaza, Antananarivo, Madagascar by Brusca et al. (in press).

Diagnosis

Fronal lamina usually elongate (in two Pacific species as long as wide), anterior margin projecting or sessile; pentagonal or with anterior margin rounded or truncate. Antennule with peduncular articles 1 and 2 usually coalesced. Pereopods all ambulatory. Pleopod 2 of male with appendix masculina basally or sub-basally inserted, usually robust; endopods of pleopods 3-5 without plumose marginal setae, smaller than exopod; lamellar or thickened (*A. barndardi*, *A. oaxaca*). Mouthparts and other characters as for *Cirolana.*

Remarks

Anopsilana, with little question, constitutes a polyphyletic assemblage of species, differing from *Cirolana* primarily in the lack of marginal setae on the endopods of pleopods 3 and 4. These endopods are also reduced in size in comparison to those of *Cirolana* and in at least two species are thickened or fleshy. Other minor differences, none of which are shown by all of the species placed in the genus, are the fusion of peduncular articles 1 and 2 of the antennule; article 3 of the antennule peduncle being proportionally longer than in *Cirolana* and the appendix masculina varying from being relatively robust to slender and basally inserted.

Estuarine species tend to be well pigmented and have robust well-spined pereopods that are generally similar to those of the *Cirolana* '*parva* group' or 'tuberculate group' of species. Troglobitic species have relatively more slender pereopods with, by comparison, reduced spination. Additionally all the troglobitic species lack eyes.

The distribution of the genus is restricted to tropical localities. The cavernicolous species are from the peri-Caribbean region except for one species from Madagascar and one from Palau. The open-water species are all estuarine, tropical and all have been recorded from mangroves or in the vicinity of mangroves, with the exception of the poorly known *Anopsilana luciae*. *Anopsilana pustulosa* and *A. willeyi* have extensive Indo-Pacific distributions. Brusca et al. (in press) report that *A. browni* is widely distributed in the Caribb-

ean and also in the tropical East Pacific in suitable habitats.

KEY TO AUSTRALIAN SPECIES OF *ANOPSILANA*

1. Body with nodules on dorsal surfaces of pereon, pleon and pleotelson; pleotelson apex narrowly rounded; endopods of pleopods 3-5 lamellar.....2

   Body without dorsal ornamentation; pleotelson apex wide, subtruncate; endopods of pleopods 3-5 fleshy.....*A. barnardi* sp.nov.

2. Frontal lamina anterior margin rounded; pleotelson abruptly narrowed; uropod rami with dense mass of marginal setae.....*A. pustulosa*

   Frontal lamina pentagonal; lateral margins of pleotelson not abruptly narrowed; uropod rami with single rank of marginal setae.....*A. willeyi*

Anopsilana barnardi sp.nov.

MATERIAL EXAMINED

HOLOTYPE: ♂ (5.4mm), Murray R., north Queensland, 18°16'S, 146°01'E, 24 May 1978, salinity of 23-34‰, depth 1.5m, mid-estuary, mud bottom, coll. P. Davie (QM W17263).

PARATYPES: 13♂♂ (2.9-5.7mm, m = 3.9m, 5.7mm specimen dissected), 14♀♀ (3.0-5.9mm non-ovig, m=4.0mm; 6.4mm ovig), manca (2.7mm), same data as holotype (QM W17264).

DESCRIPTION

Male: Body about 2.8 times as long as greatest width; dorsal surfaces without nodules, unornamented. Cephalon with median rostral point visible in dorsal view; dorsal interocular furrow present; eyes together about 0.3 width of cephalon. Pereonite 1 about 1.6 times as long as pereonite 2; pereonite 2>3>4<5 = 6>7 in length; pereonite 7 shortest. Coxae of pereonites 2-7 each with distinct and entire oblique carina; coxae 4-7 with posteroventral angle becoming increasingly acute. Pleonite 1 concealed by pereonite 7; pleonite 3 with lateral margins posteriorly produced and overlapping lateral margins of pleonite 4 which are produced posteriorly beyond pleonite 5. Pleotelson 0.65 as long as anterior width; lateral margins convex, posterior margin subtruncate, provided with 8 (or 9, see Variation) spines, interspersed with 2 short setae between each spine pair.

Antennule peduncle articles 1 and 2 fused, article 3 about 1.2 times as long as fused articles 1 and 2; flagellum extending to middle of pereonite 1, with 8 articles, the distal 2 being minute, about 0.7 as long as peduncle. Antennal peduncle article 4 about 2.5 times as long as article 3; peduncular article 5 about 1.2 times as long as 4; flagellum extending to pereonite 4, composed of about 17 articles. Frontal lamina pentagonal, sessile; lateral margins diverging anteriorly. Mandible lacking lacinia mobilis; spine row with 9 spines; molar process very thin, with 13 or 14 teeth; palp article 2 with 12 serrate setae on distolateral margin, article 3 with 14 setae distal 3 of which are longer than remaining 11 and feebly serrate, others obviously serrate. Maxillule with 12 spines on gnathal surface of lateral lobe; medial lobe with 3 stout moderately plumose spines. Maxilla with 5 long setae on lateral lobe, 9 long setae on central lobe, medial lobe with 4 stout plumose setae proximally, distally 6 simple setae. Maxilliped with simple setae only; endite with 2 coupling hooks and 4 plumose setae.

Pereopod 1 basis with 1 long and 1 short seta at posterodistal angle; ischium with 2 setae at anterodistal angle, 2 small setae at posterodistal lateral margin and 1 spine at posterodistal medial margin; merus with 4 short stout tubercular spines on lateral posterior margin and 5th longer spine at posterodistal angle, posterior medial margin with 2 acute spines; carpus with single acute spine and 3 setae at posterodistal angle; propodus palm with 2 acute spines and third stout spine and 2 setae opposing dactylus. Pereopods 2 and 3 similar to 1 but less robust. Pereopod 2 ischium with 2 acute spines at anterodistal angle and 2 stout spines at posterodistal angle; merus with 2 large and 2 small spines at anterodistal angle, posterodistal margin with 6 blunt spines in 2 clusters; carpus with 3 spines at posterodistal angle; propodus with single spine on palm. Pereopods 4-7 essentially similar, becoming longer posteriorly. Pereopod 7 ischium with group of 5 spines at anterodistal angle, posterior margin with 3 groups of spines; merus with clusters of 6 and 4 spines at distal angles, 3 spines set posteromedially; carpus with abundant spines on distal margin (about 13), 1 and 2 spines set on posterior margin; propodus with 2 pairs of spines on posterior margin; some spines on anterior margins strongly pectinate; spines on posterior margin all simple. Penes small, inconspicuous (only easily visible on dissected male paratype) papillae, set submedially on posterior of sternite 7.

Pleopod 1 rami subequal length, endopod slight-

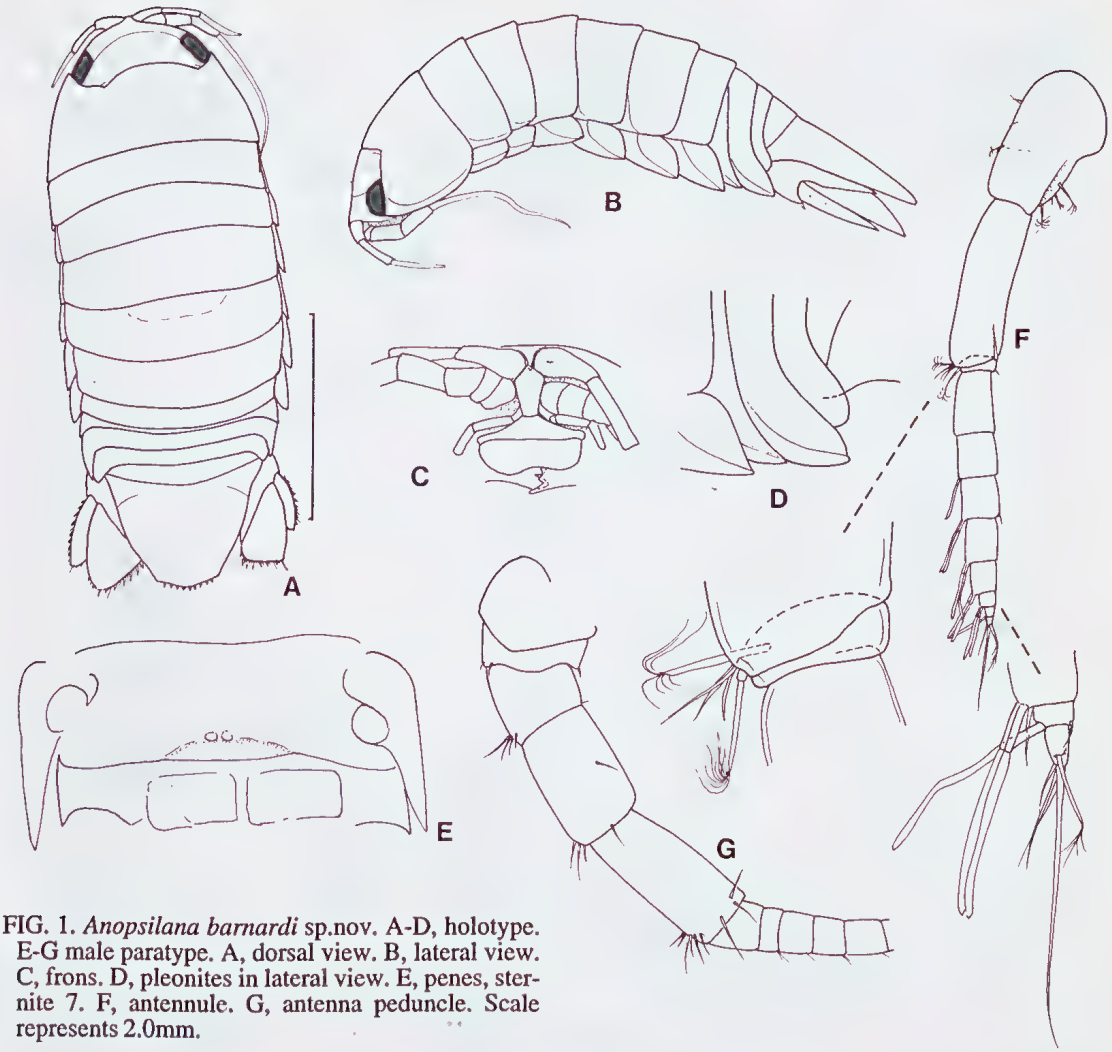

FIG. 1. *Anopsilana barnardi* sp.nov. A-D, holotype. E-G male paratype. A, dorsal view. B, lateral view. C, frons. D, pleonites in lateral view. E, penes, sternite 7. F, antennule. G, antenna peduncle. Scale represents 2.0mm.

ly less than half as wide (0.45) as exopod; peduncle about 1:8 as wide as long, medial margin with 4 coupling hooks. Pleopod 2 with rami subequal in length; appendix masculina broad, 0.3 as wide as endopod, arising basally and extending just beyond end of endopod. Pleopods 3-5 exopod with complete but faint suture; endopods fleshy and small, about 0.5 as wide and 0.7 as long as exopods. Uropod rami not extending beyond posterior of pleotelson, exopod 0.85 as long as endopod; exopod lateral margin with 9 spines, medial margin with 6; endopod lateral margin with 3 spines, medial with 7; peduncle with 2 spines at lateroventral angle; apices of both rami weakly bifid; both rami with plumose marginal setae among spines except for proximal three quarters of lateral margin of endopod.

Female: Slightly larger than male, differs in secondary sexual characters. Brood pouch made up of overlapping oostegites arising from sternites 1-5; embryos within dorsally oriented infolding of sternites.

Colour: Pale brown in alcohol, dorsal surfaces with brown chromatophores; eyes black.

Size: Males average at 3.9mm, non-ovigerous females at 4.0mm.

Variation: There is considerable variation in the number of spines present on the pleotelson and uropodal rami. The commonest spine counts are: pleotelson with 8 spines (47.6%) or 9 spines (33.3%), occasionally 7 or 10; exopod lateral margin with 7-10 spines, 9 spines (50.0%) or 8 spines (35.7%) commonest; exopod medial margin with 5 (71.4%) or 6 (19.0%) spines; endopod lateral

FIG. 2. *Anopsilana barnardi* sp.nov., male paratype. A, left mandible. B, right mandible, incisor. C, maxillule. D, maxilla. E, maxilliped. F, pereopod 1. G, pereopod 2.

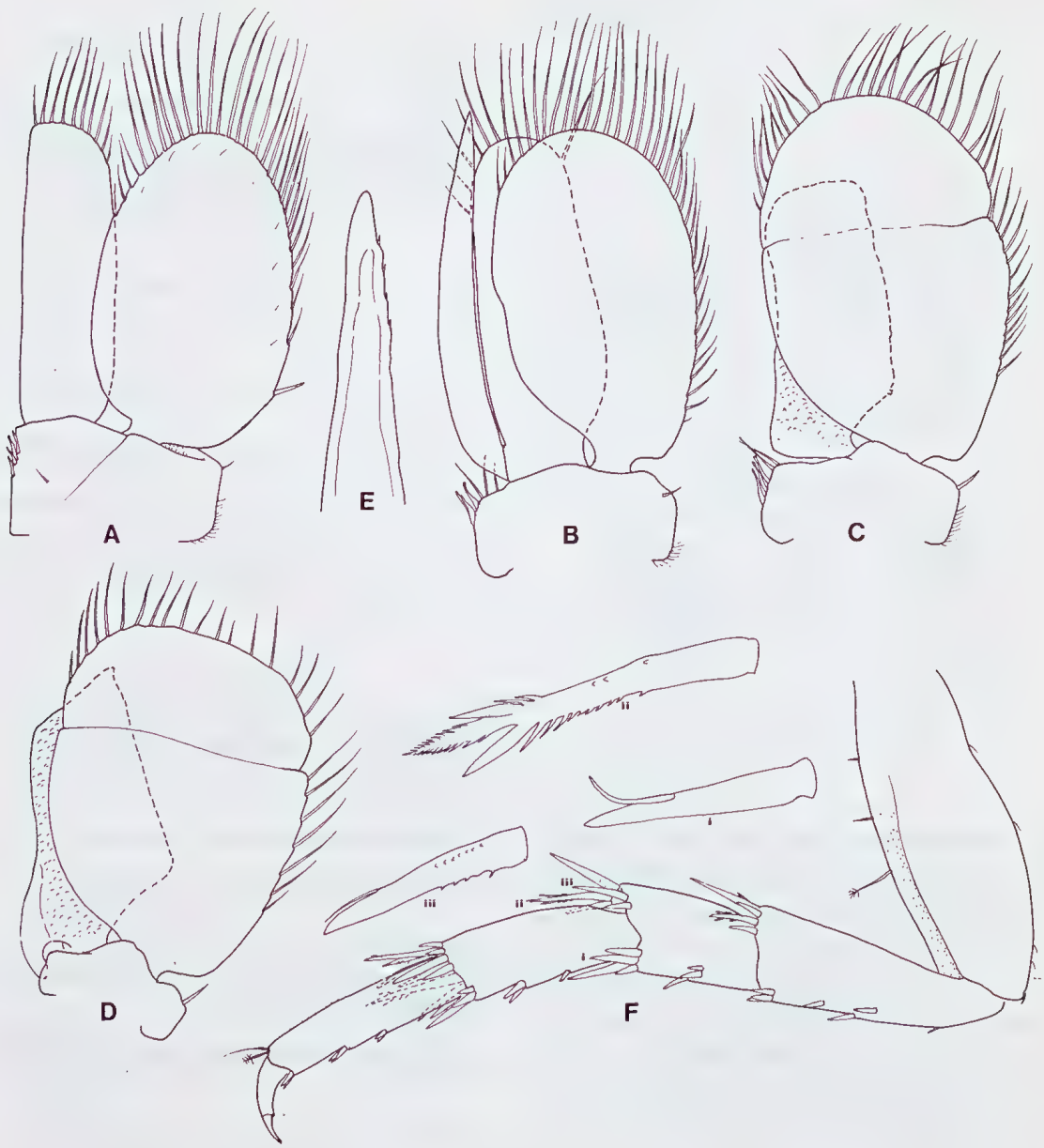

FIG. 3. *Anopsilana barnardi* sp.nov., male paratype. A-D, pleopods 1-3, 5 respectively. E, apendix masculina apex. F, pereopod 7.

margin with 3 (60%) or 4 (40%) spines, medial margin with 5 (15.0%), 6 (57.5%) or 7 (27.5%) spines (the holotype, 10 males and 10 females were examined for spine counts).

REMARKS

This species is easily separated from the two other Australian species by the lack of nodules or other cuticular ornamentation. The pleopods of *Anopsilana barnardi* have the endopod of pleopods 3-5 far smaller than those of *A. pustulosa* Hale (see Bruce 1981, fig. 5i-l) or *A. willeyi* Stebbing (see Bruce 1986, fig 138), and furthermore the endopod is thickened and semi-opaque,

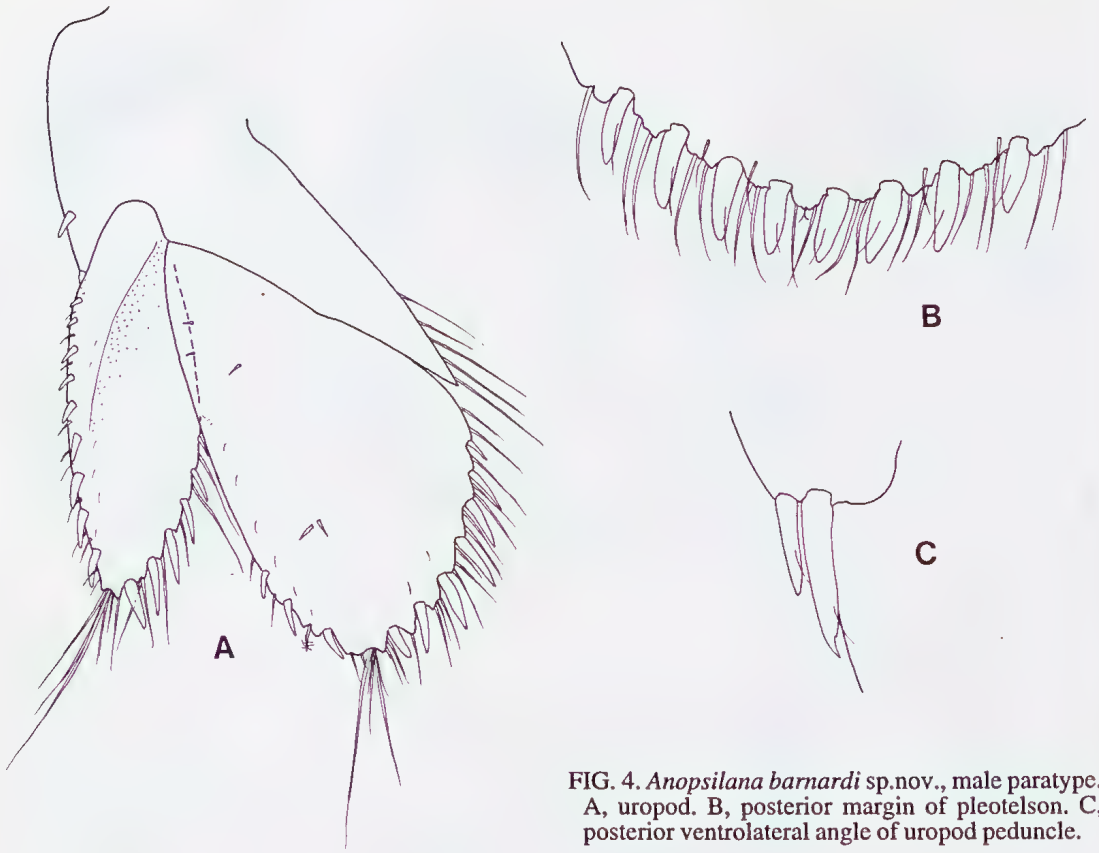

FIG. 4. *Anopsilana barnardi* sp.nov., male paratype. A, uropod. B, posterior margin of pleotelson. C, posterior ventrolateral angle of uropod peduncle.

not lamellar. There are only two other Indo-Pacific species of *Anopsilana*: *A. lingua* Bowman & Iliffe, 1987, which is a blind freshwater cave dwelling species from Palau, and *A. luciae* (Barnard, 1940) a poorly described estuarine species from South Africa. *Anopsilana luciae* differs by having a rounded projecting frontal lamina, a narrow pleotelson apex and two longitudinal submedian carinae on the pleotelson. It is possible that some estuarine species currently placed in *Cirolana* may prove to belong to *Anopsilana* when the pleopods have been examined.

ETYMOLOGY

The species is named to honour the late Dr J.L. Barnard who has made an immense contribution to the knowledge of Australian peracarid Crustacea.

SYNOPSIS OF *ANOPSILANA* SPECIES

Anopsilana acanthura (Notenboom, 1981)

DISTRIBUTION: Known only from a well in Haiti.

TYPES: Zoölogisch Museum, Amsterdam.

Anopsilana browni (Van Name, 1936)

DISTRIBUTION: Brackish and freshwater; Caribbean; Cuba and Belize; East Pacific: Costa Rica (Kensley & Schotte, 1989).

TYPES: American Museum of Natural History, New York.

Anopsilana crenata Bowman & Franz, 1982

DISTRIBUTION: Freshwater pool in a cave, Grand Cayman Island.

TYPES: Smithsonian Institution.

Anopsilana cubensis (Hay, 1903)

DISTRIBUTION: Caves in several localities in Cuba.

TYPES: Smithsonian Institution.

Anopsilana jonesi Kensley, 1987

DISTRIBUTION: Amongst mangroves, Belize.

TYPES: Smithsonian Institution.

Anopsilana lingua Bowman & Iliffe, 1987

DISTRIBUTION: Natural well on Peleliu Island, Palau.

TYPES: Smithsonian Institution.

Anopsilana luciae (Barnard, 1940)

DISTRIBUTION: Estuarine, South Africa.

TYPES: South African Museum, Cape Town.

Anopsilana oaxaca Carvacho & Haasmann, 1984

DISTRIBUTION: Mangroves roots, Pacific coast of Mexico; also Clipperton Island (Brusca et al. in press).

TYPES: Institute of Biology, National Autonomous University of Mexico.

Anopsilana poissoni Paulian & Deboutteville, 1956

DISTRIBUTION: Mitoho Cave, southern Madagascar.

TYPES: Not stated, but see type species entry after genus synonymy given here.

Anopsilana pustulosa (Hale, 1925)

DISTRIBUTION: Estuarine and mangrove habitats from East Africa to Australia; generally within the tropics (Bruce, 1986). Type locality: Cooktown, Queensland.

TYPES: Australian Museum, Sydney.

Anopsilana radicicola (Notenboom, 1981)

DISTRIBUTION: Natural spring, Haiti.

TYPES: Zoölogisch Museum, Amsterdam.

Anopsilana willeyi (Stebbing, 1904)

DISTRIBUTION: Estuarine and mangrove habitats from East Africa to Australia, within the tropics (Bruce, 1986). Type locality: Sri Lanka (Stebbing, 1904, as Ceylon).

TYPES: Not located.

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SYSTEMATICS OF THE INTERTIDAL TRAPDOOR SPIDER GENUS *IDIOCTIS* (MYGALOMORPHAE: BARYCHELIDAE) IN THE WESTERN PACIFIC WITH A NEW GENUS FROM THE NORTHEAST

TRACEY B. CHURCHILL AND ROBERT J. RAVEN

Churchill, T. B. & Raven, R. J. 1992 06 29: Systematics of the intertidal trapdoor spider genus *Idioctis* (Mygalomorphae: Barychelidae) in the Western Pacific with a new genus from the Northeast. *Memoirs of the Queensland Museum* 32(1): 9-30. Brisbane. ISSN 0079-8835.

The circum-tropical trapdoor spider genus *Idioctis* included 6 species from Madagascar, east to Hawaii. A new genus, *Nihoa*, endemic to the Leeward Islands, north of Hawaii, is named and now includes *Idioctis hawaiiensis* Raven, 1988, endemic to Necker Island, and a further new species, *Nihoa mahina* sp.nov., endemic to Nihoa Island. Four new species of *Idioctis* from the Western Pacific are described: *I. yerlata* from north-eastern Australia; *I. ferrophila* from New Caledonia; *I. marovo* from the Solomon Islands; and *I. talofa* from Western Samoa, raising the number of species to nine. For the first time, the male of the type species *I. helva* Koch, 1874, from Fiji, is described. Variation in the shape of spermathecae in *Idioctis* is described. □*Chelicerata, Mygalomorphae, Barychelidae, systematics, phylogeny.*

Tracey B. Churchill and Robert J. Raven, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 3 February, 1992.

Spiders of a number of genera occur beside the sea. However, only few are intertidal in that their burrows are covered at high tide. Best known among araneomorphs are *Desis* and *Paratheuma* (Desidae), the latter having been revised recently (Beatty and Berry, 1988). In contrast, spiders of only one mygalomorph genus, *Idioctis* Koch, 1874, are known to live in the intertidal zone.

The genus *Idioctis* was first described by Koch (1874) including only *I. helva* from Fiji. No reference was made to the habitat. The first report of the intertidal habits of a barychelid was with the description of *Idioctis littoralis* Abraham, 1924, found in the intertidal mudflats of Singapore. Much later, *I. helva* was recorded from the littoral zone in Western Samoa (Marples, 1951, 1955). Soon after, another species, *Atrophonysia intertidalis* Benoit & Legendre, 1968, (transferred to *Idioctis* by Raven, 1985) was collected and described from the littoral zone of Madagascar and the Seychelles.

By 1988, six species of *Idioctis* had been described: the type species, *I. helva* from Fiji and Western Samoa (Marples, 1951, 1955); *I. littoralis* Abraham, 1924 from Singapore; *I. intertidalis* (Benoit & Legendre, 1968) from Madagascar and the Seychelles (Benoit, 1978); *I. xmas* Raven, 1988 from Christmas Island; *I. eniwetok* Raven, 1988 from the Caroline and Marshall Islands; and *I. hawaiiensis* Raven, 1988 from the Leeward Islands, near Hawaii.

After a revision of the genus (Raven, 1988), we discovered *Idioctis* in the intertidal or littoral zones in northern Australia, New Caledonia, and the Solomon Islands. Three new species are described here. Concurrently, the first male and more females of the type species, *I. helva*, were taken from the type-locality of Ovalau, a small island of Fiji. Females of *I. helva* were also collected from the coast of the large island of Vanua Levu, Fiji. With this new material we conclude that a new species occurs in Western Samoa. We also document variation in spermathecae for the first time in barychelids.

Raven (1988) noted that *Idioctis hawaiiensis* differed from all other congeners in the wider sternum, undivided spermathecae, and relatively shorter eye group. Since then, material from another island in the Leeward Islands has proved to be a new species for which a new genus is here created. This new genus recognizes the plesiomorphic nature of both *I. hawaiiensis* and its new sister species.

MATERIALS AND METHODS

All abbreviations are standard for the Araneae and explained in Raven (1984a). The width of the eye group or the median ocular quadrangle (abbreviated as MOQ) is the distance between the two most separated points in a line orthogonal to the long axis of the spider. All measurements except those for eyes are given in millimetres. Eye measurements are taken from camera lucida drawings made at × 50 magnification; any error was taken as 0.02 mm, or 1mm on the enlarged figure. Eye interspaces, which are measured along a line joining the centres of the respective eyes, are given as

diameters of an AME. Presence of leg spines are specified by the number recorded with their position (rare number occurring in parentheses) although ranges can include zero. Spine positions are as follows : dorsal, if on or close to the midline; pro- or retrolateral, if spine bases are visible pro- or retrolaterally when viewed dorsally; ventral, if bases are visible when viewed ventrally. Spines are considered weak, and probably the equivalent of attenuate macrosetae of Coyle (1971: 329), if only marginally thicker than other setae on that surface. Despite being weaker, they are treated as spines because their number and position suggest they are the weaker form of thick spines on other species. Descriptions of scopulae give the extent (measured from the distal end of the leg segment), the density of scopula hairs, and the number of rows of setae that part the scopula hairs.

Acronyms for museums are: AMNH, American Museum of Natural History, New York; BMNH, British Museum (Natural History), London; NHW, Naturhistorisches Museum, Vienna; QM, Queensland Museum, Brisbane. Other museums are given in full.

SYSTEMATICS

Idioctis Koch

Idioctis Koch, 1874: 484 (type species by monotypy *Idioctis helva* L. Koch). Simon, 1892: 125; 1903: 914. Rainbow, 1912: 115. Roewer, 1942: 214. Bonnet, 1957: 2286. Brignoli, 1983: 129. Main, 1985: 12. Raven, 1985: 113; 1988: 2. Platnick, 1989: 93.

Atrophonysia Benoit & Legendre, 1968: 330 (type species by original designation *Atrophonysia intertidalis* Benoit & Legendre). First synonymized by Raven, 1985: 113. Brignoli, 1983: 130. Raven, 1985: 113, 1988: 2; Platnick, 1989: 93

Diagnosis

Idioctis can be distinguished from *Idiophthalma* by the narrow sternum and narrow fovea and absence of a strong rastellum, and from other barychelid genera by the relatively short but strongly trapezoidal eye group and a narrow sternum. It is also readily distinguished from *Nihoa* gen. nov. and many other barychelids in the pallid pattern-free abdominal dorsum and the elongate sternum.

Description

Carapace hirsute, without pattern. Fovea very broad, procurved or straight. Abdomen pallid, without pattern. Rastellar spines few in line overhanging fang, not on raised mounds. Maxillae usually with c.18-20 cuspules on inner anterior corner; anterior lobe and posterior heel produced. Labium wide, without cuspules. Sternum long, narrow (about 1.5 times longer than wide, rarely wider), with small, marginal sigilla, if evident. Scopulae (♀ ♀) entire on metatarsi and tarsi I and II; for full length of prolateral face of metatarsi III and only rarely present elsewhere on segment; widely parted by setae on tarsi III; only narrow lateral bands of hair, if present, on tarsi IV; absent on metatarsi IV. Scopuliform brush present on the proventral face of tibiae I and II of ♀ ♀. Spines. Leg 1: fe d0-4; ti p0-1 v2-7; me r0-1. Leg 2: fe d0-4; ti p0-1 v0-4; me v1-2. Leg 3: fe p0-1, d0-5; pa p6-30; ti p(2), r(2), v0-7; me p0-3, r0-3, v0-13. Leg 4: fe d0-7; pa p3-16; ti r(2), v0-7; me p0-7, r0-4, v2-9. Paired claws of ♀ ♀ with teeth on lateral face (Fig. 3); claws of ♂ ♂ biserially dentate. Tarsi with clavate and filiform trichobothria. ♂ ♂: tibia I with prolateral spur and megaspine, more distal prolateral megaspine and associated cuticular 'thumb'; palpal bulb pyriform. Intertidal, rarely in forests.

Checklist of Species

Idioctis helva Koch, 1874, type species Fiji.
Idioctis eniwetok Raven, 1988 Caroline & Marshall Islands.
Idioctis ferrophila sp.nov. New Caledonia.
Atrophonysia intertidalis Benoit & Legendre, 1968 Madagascar, Seychelles.
Idioctis littoralis Abraham, 1924 Singapore.
Idioctis marovo sp.nov. Solomon Islands .
Idioctis talofa sp.nov. Western Samoa.
Idioctis xmas Raven, 1988 Christmas I., Australia.
Idioctis yerlata sp.nov. North-eastern Australia.

Distribution

Spiders of the genus *Idioctis* are now known near beaches and in littoral zones in Fiji, Singapore (Abraham, 1924), Western Samoa (Marples, 1951, 1955), Madagascar (Benoit & Legendre, 1968), Seychelle Islands (Benoit, 1978), Christmas Island (Indian Ocean, Raven, 1988), Marshall and Caroline Islands (Raven, 1988), north-eastern Australia, New Caledonia and the Solomon Islands. Habitats, life history observations and biogeography of the genus will be discussed elsewhere.

Remarks

This paper contains the first description of a ♂ of the type species. The diagnosis of *Idioctis* given by Raven (1988) is correct save for the removal of

characters present only in *I. hawaiiensis*, here transferred to *Nihoa*, gen. nov.

Idioctis helva Koch
(Figs 2-6, Table 1)

Idioctis helva L. Koch, 1874: 484, tab. 37, fig. 3 a,b. Hogg, 1901: 241-242, fig. 26a. Marples, 1955: 453-454; Raven, 1988: 4, figs 1-5.

Material Examined

Lectotype: ♀, (here designated), Ovalau I., 17°41'S, 178°50'E, Fiji, Mus. Godeffroy No. 8097, deposited in Zoologische Institut and Zoologisches Museum, Hamburg.

Paralectotypes: 1♀, 1 juvenile, same data, deposited in BMNH.

Other Material

Topotypes: 1♂, Naqeledamu, Ovalau I., 17°41'S, 178°50'E, Fiji, in mangrove root, 14.xi.1988, T.B. Churchill, QM S11229. 5♀♀, Naqeledamu, Ovalau I., Fiji, 14.xi.1988, T.B. Churchill, QM S12521-5; 6♀♀, Lotu I., Vanua Levu, 16°46'S, 179°20'E, Fiji, 20.x.1988, T. B. Churchill, QM S12526-30.

Diagnosis

Spermathecae two, each consisting of two short dissimilar lobes, ental lobe stout, ectal lobe slender. ♀♀ with c.18 thorns on patella III. 4-5 teeth on paired claws of ♀♀. Rastellum of ten thick (four as long as wide) coniform spines in short distal line. Preening combs absent. ♂♂. Tibia I with small distal spur and upcurved megaspine, prolateral face with distal triangular cuticular process and short lower angular downcurved spine. Bulb pyriform; embolus broad, not spiralled; cymbium with two divided lobes. Two rows of teeth on all paired claws.

TABLE 1. Leg measurements of *Idioctis helva*, ♂.

	I	II	III	IV	Palp
Femur	3.60	3.20	2.56	3.36	2.20
Patella	1.92	1.84	1.44	1.76	1.44
Tibia	3.04	2.64	2.16	3.52	1.52
Metatarsus	2.32	2.16	2.16	2.96	
Tarsus	1.36	1.28	1.20	1.20	0.84
Total	12.24	11.12	9.52	12.80	6.00

Topotype Male

Carapace 4.36 long, 3.32 wide. Abdomen 4.16 long, 2.40 wide. Total length, 10.

Colour in alcohol. Carapace and legs yellow brown, chelicerae red brown; abdomen dorsally grey brown with dark 'V' dorsally showing location of heart; venter entirely yellow brown.

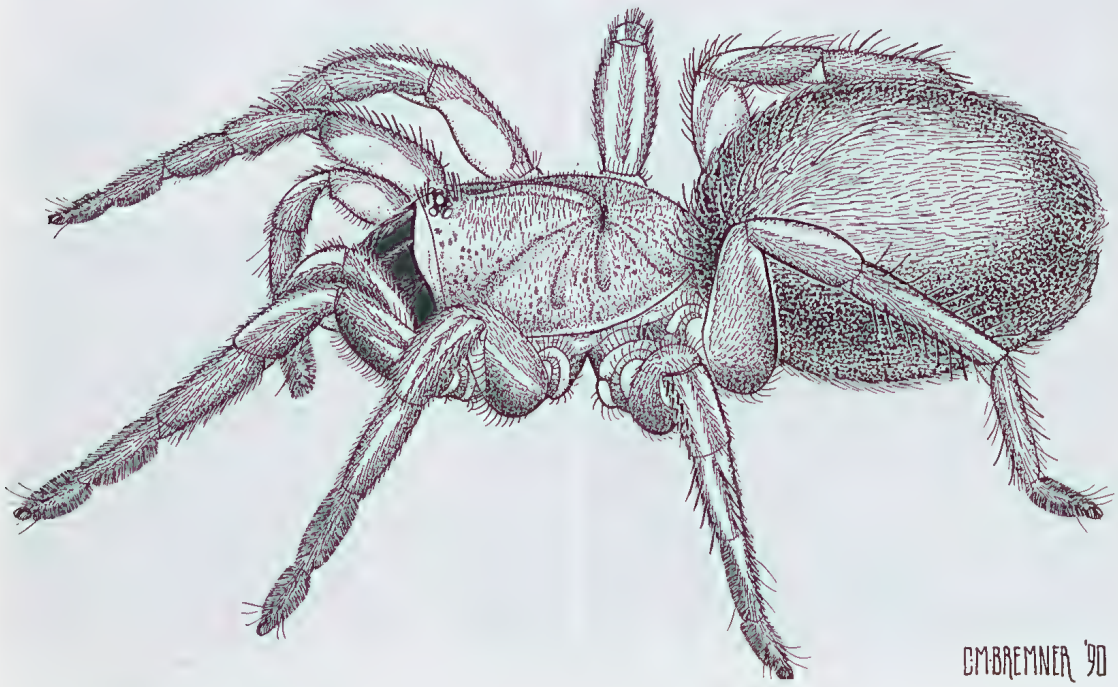

FIG. 1. *Idioctis yerlata* sp.nov., ♀.

FIG. 2. Distribution of *Idioctis* ★ and *Nihoa* ▲ in the Western Pacific and Indian Ocean.

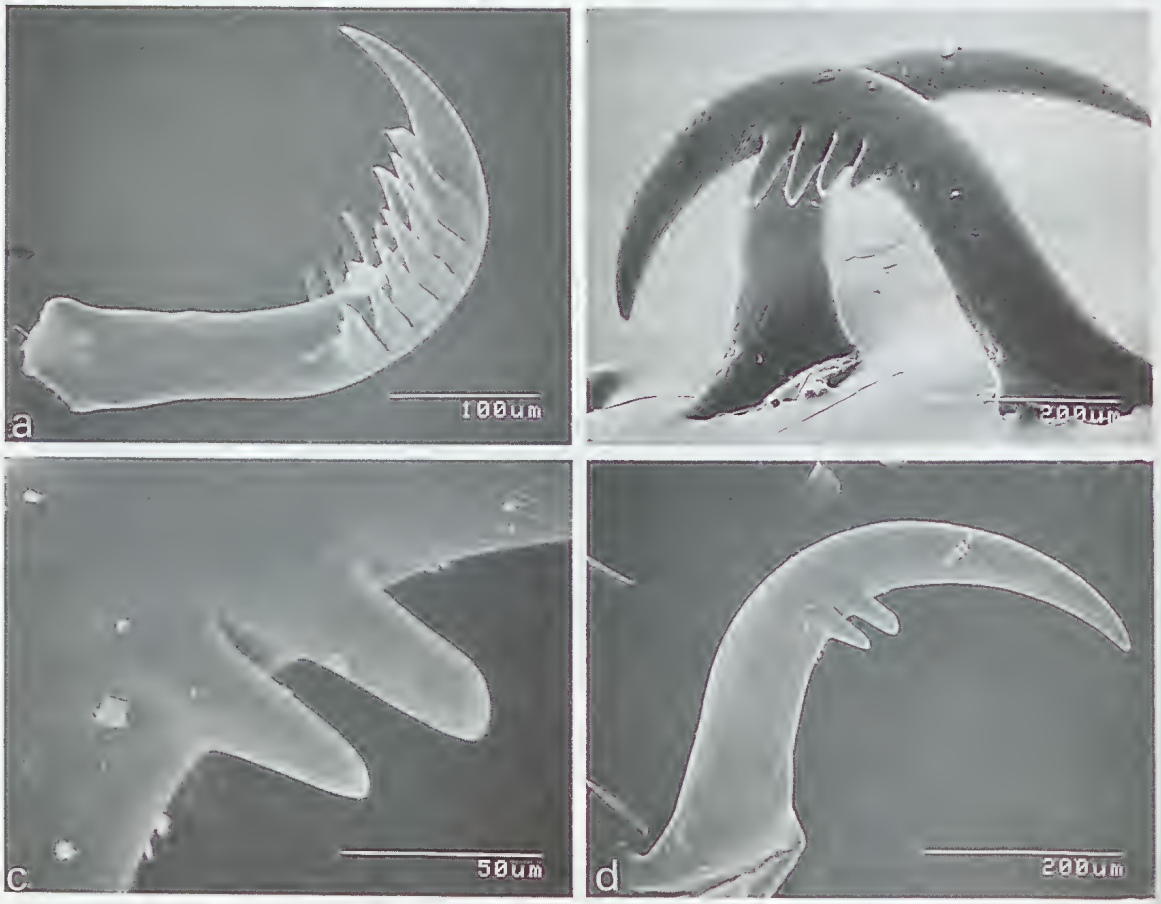

FIG. 3. *Idioctis helva*, scanning electron micrographs, paired claws, lateral view. a, b, leg I, ♂ (a), ♀ (b). c, d, leg IV, ♀.

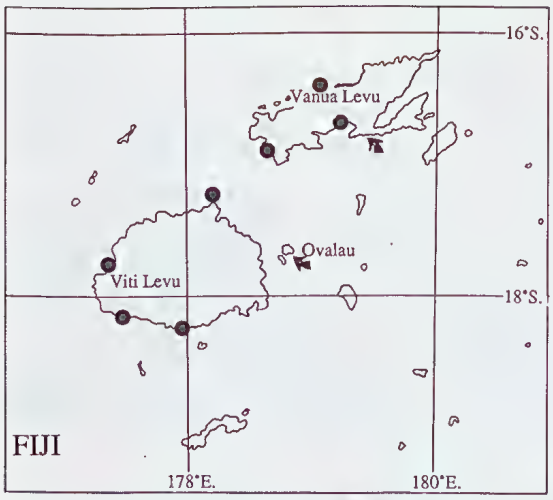

FIG. 4. Presence ➨ and absence ● of *Idioctis helva* at coastal localities sampled in Fiji.

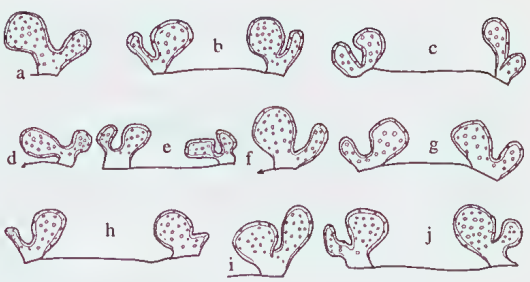

FIG. 5. *Idioctis helva*, dorsal view of spermathecae of ♀♀. a-d, g, Ovalau Island, Fiji. a, S12525. b, S12521. c, S12522. d, S12523. g, S12524. e, f, h-j, Lotu Island (Vanua Levu), Fiji. e, S12527. f, S12528. h, S12526. i, S12529. j, S12530. Scale line = 0.25mm.

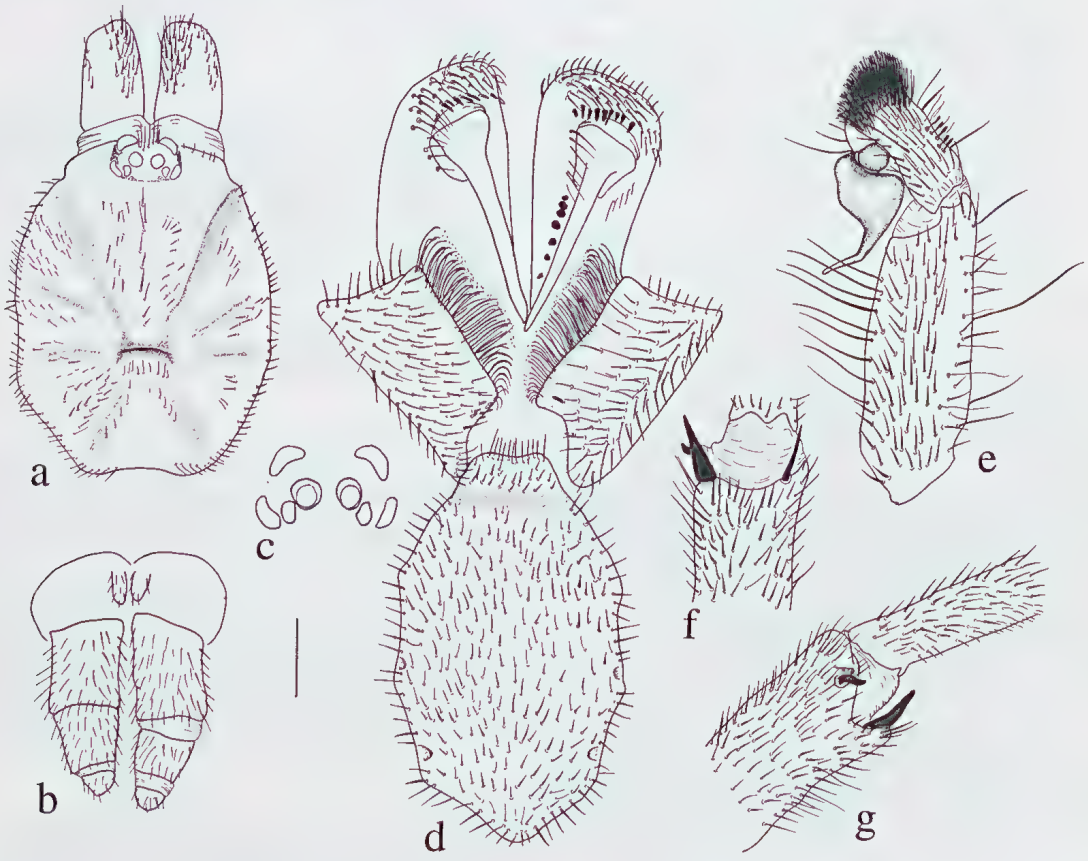

FIG. 6. *Idioctis helva*, topotype ♂. a, cephalothorax and chelicerae, dorsal view. b, spinnerets, ventral view. c, eyes, dorsal view. d, sternum, maxillae, labium and chelicerae, ventral view. e, palpal tibia, cymbium, and bulb, retroventral view. f, tibia I, ventral view, showing distal spur and megaspine. g, tibia I showing spur, prolateral view. Scale line = 1mm (a), 0.5mm (b-g).

Carapace. Uniform covering of short black bristles and fine grey hair, not obscuring cuticle; margins with longer setae and lower sclerotised shelf of hirsute chitin below main margin. An irregular row of 15-20 setae anteromedially; 2-3 pairs of fine setae; numerous thick setae between PME and ALE. Striae shallow, narrow, glabrous, recognised as areas intervening grey bush of hair. Fovea wide, recurved.

Eyes. Tubercle distinct. Group occupies 0.45 of head-width. Three rows; back row recurved. Front line of lenses of AME just behind line of back of ALE and 'iris' well back. Eye group front width, back width, length = 35:43:25. MOQ front width, back width, length = 21:29:14. AME:ALE:PME:PLE = 10:11:7:10. Eye interspaces:AME-AME, 0.5; AME-ALE, 0.5; ALE-ALE, 1.6; PME-PLE, 0.2; PME-PME, 1.8; ALE-PLE, 0.6.

Chelicerae. Wide band of brown setae and grey hair prodorsally, two narrower bands laterally. Promargin with 8 evenly spaced teeth, basomesally with 2 small teeth and 3 granules. Intercheliceral tumescence absent. Rastellum consists of 5 long thick pointed spines and c.5 thick setae.

Labium. 0.64 wide, 0.28 long. Cuspules absent. Labiosternal suture is two sigilla narrowed at their medial junction.

Maxillae. 1.04 long in front, 1.36 long behind, 0.64 wide; with c.5-8 pointed cuspules. Heel angular; anterior lobe distinct.

Sternum. 2.16 long, 1.48 wide. Only posterior sigilla evident as rounded glabrous marginal areas.

Legs. Formula 4123. All segments, especially femora, with mat of dark grey prostrate hairs; and erect black setae. All legs of similar diameter. Tibia I with small distal spur and upcurved megaspine, prolateral face with distal triangular cuticular process and short lower angular downcurved spine. Preening combs entirely absent.

Scopula. Never so thick as to obscure cuticle, individual hair bases distinct. Tarsi I-III ventrally pallid. Tarsi:I and II entirely ventral, thin, entire, full length; III, thin, divided by 8-10 setae; IV, with 10-15 scopula hairs in narrow triangle on proximal prolateral face. Claw tufts smaller than claws. Metatarsi: I, thin for full length, distally cuticle is pallid; II, similar but with single thick seta on ventrodistal edge; III, proventrally with light brush; IV, bare. Thorn spines: 10 on prolateral patella III.

Spines. Leg 1: fe d4, ti v3 +2 megaspines; me v1 weak, distal. Leg 2: fe d3, ti v4; me v1 weak, distal. Leg 3: fe d4, r1, pa p10 thorns, ti v5, me r1, v4. Leg 4: fe d6, r1w; ti r2, v7w; me v3 + 4 thick setae. Palp: fe d5w.

Claws. 2 full scooped rows of 8-10 teeth in each row on paired claws of leg I; claws of leg IV with 2 rows, 6 in each outer row and 2 in each inner row.

Trichobothria. In two rows, each of c.8 for 3/4 of tibiae; c.12 in proximally retrolateral row on metatarsi, distally row is irregular and trichae are longer; c.3 clavate and 15 filiform on tarsi in band.

Palp. Bulb pyriform; embolus broad, not spiralled; cymbium with two divided lobes.

Spinnerets. PMS 0.20 long, 0.08 wide, 0.08 apart, c.0.18 of basal PLS in diameter. PLS basal, middle, apical, and total article lengths = 0.64, 0.26, 0.14, 1.04, respectively.

Distribution and Habitat

I. helva is known from mangrove roots and trunks on Ovalau Island, east of Viti Levu, Fiji, and from coral rock on Lotu Island, south of Vanua Levu, Fiji.

Remarks

Females of *I. helva* differ from those of other species by the wider configuration of the eyes and the smaller PMS. Spermathecae consist of two short almost amorphous lobes joined basally to form a common aperture. Males differ from those of *I. eniwetok* Raven by the absence of preening combs.

Idioctis yerlata sp.nov.
(Figs 1, 2, 7-9, Table 2)

Material Examined

Holotype: ♀, Cape Tribulation, 16°05'S, 145°26'E, in mangroves, North Queensland, Australia, 28-29.viii.1988, R.J. Raven, T.B. Churchill, J.A. Gallon, QM S7213.

Paratypes: 7♀♀, Cape Tribulation, 16°05'S, 145°26'E, in mangroves, North Queensland, 28-29.viii.1988, R.J. Raven, T.B. Churchill, J.A. Gallon, QM S7204-9, S7212, S11181. 1♀, Noah Head, S. of Cape Tribulation, 16°08'S, 145°28'E, 30.viii.1988, R.J. Raven, T.B. Churchill, J.A. Gallon, QM S7206.

Diagnosis

Spermathecae with one large medial lobe and variable basal lobe ectally; basal lobe small with common atrium with lateral lobe or separate lobe arising above base of medial lobe (Fig. 9). Three closely spaced teeth on cheliceral promargin near fang base. Numerous (28-30) thorn spines on prolateral patellae III. 5-7 teeth on paired claws of

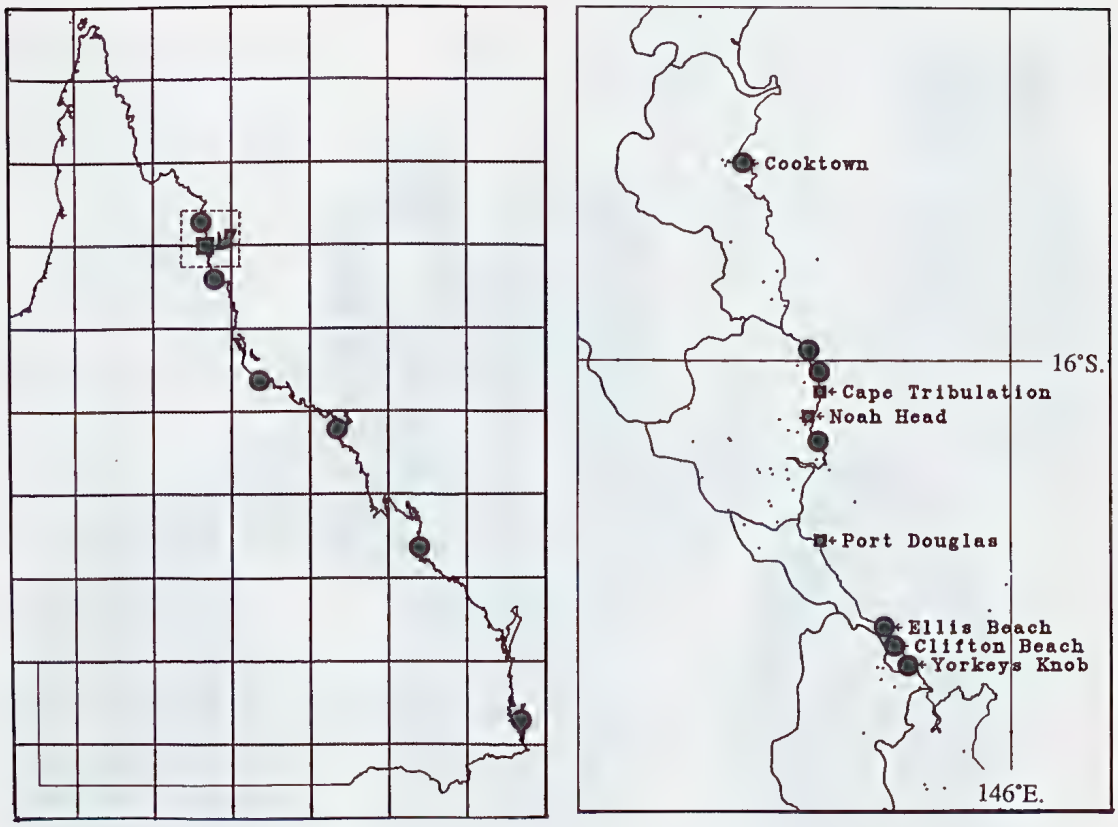

FIG. 7. Presence of *Idioctis yerlata* sp.nov. at coastal localities sampled in Queensland, Australia; inset enlarged at right, presence ■ and absence ●.

leg I. Preening combs absent. Rastellum is 12-14 long curved spines.

HOLOTYPE FEMALE

Carapace 5.36 long, 4.40 wide. Abdomen 8.80 long, 5.28 wide. Total length, 16.

Colour in alcohol and life. Carapace and legs yellow brown, chelicerae red brown, abdomen uniform yellow brown.

Carapace. Uniform cover of fine prostrate wavy grey hairs; 10-15 long erect setae on medial caput lateral of centre line; c.4 pairs of fine foveal bristles; 27 long erect black setae anteromedially; 7 long black anteriorly directed bristles and numerous fine black setae between PME; 2 long recurved and 10-15 shorter black bristles between ALE; caput raised; striae distinct. Fovea broad, straight with recurved ends.

TABLE 2. Leg measurements of *Idioctis yerlata*, holotype ♀

	I	II	III	IV	Palp
Femur	3.28	2.88	2.24	3.44	2.64
Patella	2.48	2.32	1.84	2.64	1.84
Tibia	2.48	2.24	1.84	3.44	1.64
Metatarsus	1.84	1.76	1.12	2.80	
Tarsus	1.36	1.20	0.88	1.20	1.52
Total	11.44	10.40	7.92	13.52	7.64

Eyes. Tubercle low. Group occupies 0.33 of head width. Three rows; back row more or less straight. Eye group front width, back width, length = 44:58:34. MOQ front width, back width, length = 23:42:17. AME:ALE:PME:PLE = 7:13:7:15. Eye interspaces: AME-AME, 1.3; ALE-ALE, 3.4; AME-ALE, 1.6; PME-PLE, 0.1; PME-PME, 4.0; ALE-PLE, 1.6.

Chelicerae. With moderately dense bush of black hairs dorsally and in lateral band; rastellum consists of 12-14 long strong spines; promargin of furrow with two very large and five smaller teeth, and six small teeth basally.

Labium. 0.92 wide, 0.48 long, without cuspules, separated from sternum by narrow groove.

Maxillae. 1.60 long in front, 2.04 long behind, 0.96 wide; with 6-9 spindle-shaped cuspules in

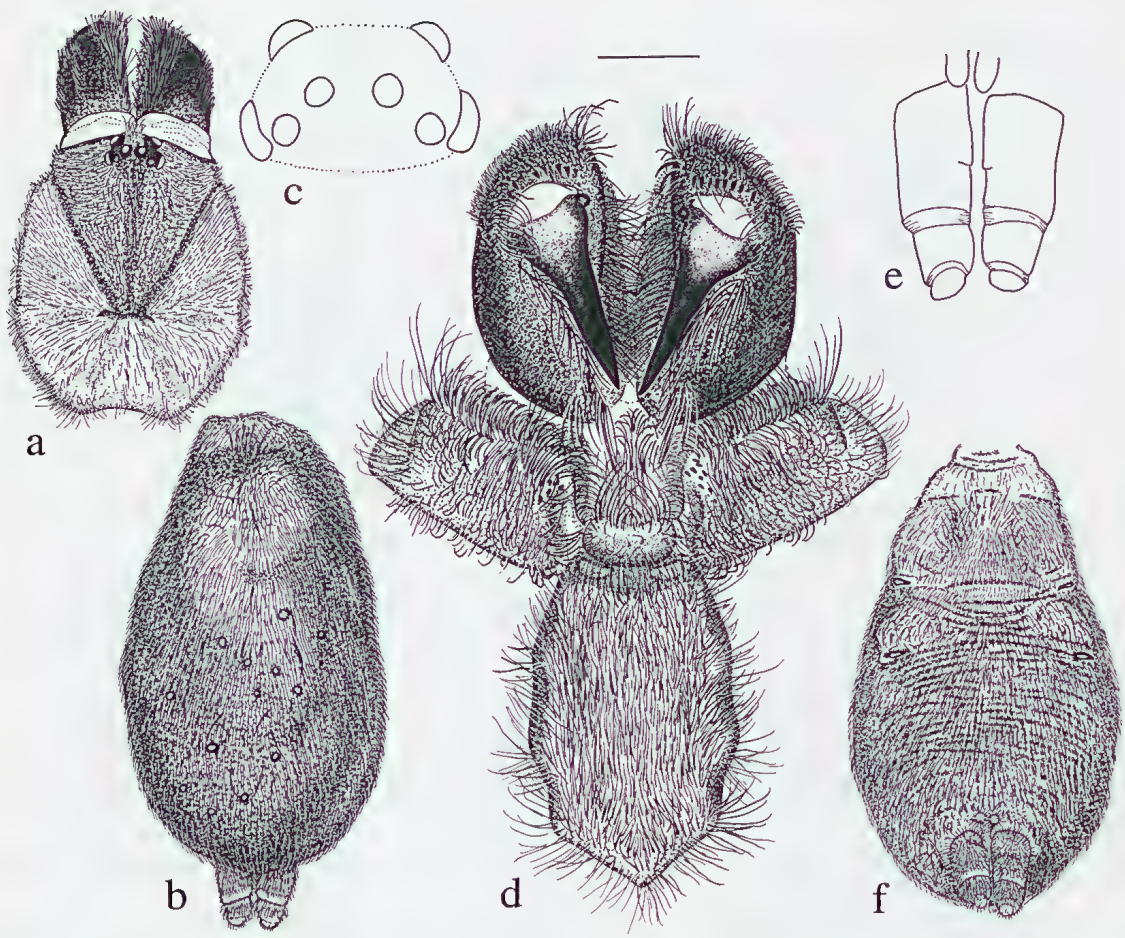

FIG. 8. *Idioctis yerlata* sp.nov. holotype ♀. a, cephalothorax and chelicerae, dorsal view. b, abdomen, dorsal view. c, eyes, dorsal view. d, sternum, maxillae, labium and chelicerae, ventral view. e, spinnerets, ventral view. f, abdomen, ventral view. Scale line = 2 mm (a, b), 1mm (d), 0.5mm (c, e).

close group on inner angle; anterior lobe indistinct, posterior 'heel' produced.

Sternum. 3.12 long, 2.00 wide; sigilla evident as shallow depressions in margin.

Legs. Formula 4123. Legs I and II much thicker than III and IV; tarsi as fat as distal metatarsi. Dorsal tarsi and metatarsi with pile of short straight grey hair. Tibia through tarsus IV asetose, almost glabrous. With numerous short coniform spines on prolateral patellae III, IV. Preening combs consist of group of 8 spines on metatarsi III, outer pair and middle pair long and slender, others short, thick; eight also on metatarsi IV, two long slender setae separated by shorter spines on ventral edge of metatarsi IV.

Scopula. Full and entire on metatarsi and tarsi I, II; divided by setae on metatarsi and tarsi III; one narrow prolateral band on tarsi IV; elsewhere absent. Palpal tarsal scopulae entire.

Spines. No spines on tarsi. Leg 1: fe 0, (d11 thick setae); ti p1 weak, v7 weak; me v1 distally with thick bristle. Leg 2: me v2 distally 1v with thick bristle. Leg 3: pa p28-30; tibia v1 + 6w, me distoventral 2 long medial with 4 on each side and one between 2 long. Leg 4: fe 0, pa p11-16, ti v5, me 0. Palp, ti v1 or v0.

Claws. Paired claws with 5-7 teeth on ectally displaced keel on leg I; 3 teeth on leg III; 2 on leg IV; palpal claw without teeth. All paired claws extending beyond tufts, except on palp.

Trichobothria. c.8 for 3/4 of tibiae; c.12 on metatarsi; 5 clavate and 12 filiform on tarsi.

Spermathecae. Two, each with one large medial and one ectal lobe.

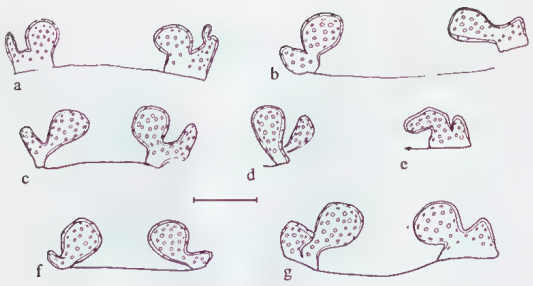

FIG. 9. *Idioctis yerlata* sp.nov., dorsal view of spermathecae of ♀♀. a, S7204. b, S7207. c, S7212. d, S7213. e, S11181. f, S7206. g, S7208. Scale line = 0.25mm.

Spinnerets. PMS 0.48 long, 0.22 wide, bases 0.10 apart, c.0.24 of basal PLS in diameter. PLS basal, median, and apical total article lengths = 1.14, 0.60, 0.20, 1.94, respectively.

DISTRIBUTION AND HABITAT

Known only from mangroves and loose coral rubble in the intertidal zone near Cape Tribulation, north Queensland, Australia. A trapdoor burrow like that of *Idioctis* was noted in the intertidal zone on a mangrove tree just south of Port Douglas, about 30km north of Cairns, north Queensland.

ETYMOLOGY

The specific epithet is an aboriginal work meaning oyster, which is often the impression conveyed by the door of *I. yerlata* burrows.

REMARKS

Females differ from all species of *Idioctis* in the larger relative size (3.4 times an AME diameter) of the ALE-ALE interspace.

Idioctis ferrophila sp.nov.
(Figs 2, 10-12, Table 3)

MATERIAL EXAMINED

HOLOTYPE: ♀, Port Boisé, 22°20'S, 166°59'E, New Caledonia, ironstone boulder in water on beach, 25.x.1988, R.J. Raven, T.B. Churchill, QM S13537.

PARATYPES: 7♀♀, Port Boisé, 22°20'S, 166°59'E, New Caledonia, ironstone boulder in water on beach, 25.x.1988, R.J. Raven, T.B. Churchill, QM S12511-3, S12515-7, S13538; 3♀♀, same data, 6.ix.1990, P. Goloboff, N. Platnick, R.J. Raven, AMNH.

DIAGNOSIS

Spermathecae with large medial lobe and short basal lobe with axes perpendicular. Thorn spines: c.30 on prolateral patellae III, c.11 small on proximal prodorsal patella IV. 3-5 teeth on paired claws of ♀♀. Rastellum a line of 10 short conical spines, not on mound, on edge above fang. ♂♂ unknown.

HOLOTYPE FEMALE

Carapace 5.28 long, 4.12 wide. Abdomen 8.48 long, 4.88 wide. Total length, 17.

Colour in alcohol and life. Carapace yellow brown with light brown mottling, chelicerae dark reddish brown-burgundy; legs, sternum, maxillae, and labium yellow brown; abdomen light yellow brown with slightly darker medial band over heart.

Carapace. With fine gray hairs forming uniform covering; hairs become larger and paler on margins and darker and thicker near anteromedial line. Striae glabrous, narrow, barely distinct. Narrow sclerotised and hirsute ledge below edge of carapace. Fovea very slightly procurved. About 10 thick and several finer anteromedial setae; two long setae between PME; 5-8 long recurved and several shorter setae and fine hairs between ALE. Clypeus absent.

Eyes. Tubercle low. Group occupies 0.32 of head-width. Three rows; back row procurved. Eye group front width, back width, length = 44:55:32. MOQ front width, back width, length = 25:33:19. AME:ALE:PME:PLE = 10:14:8:14. AME-AME, 0.4, AME-ALE, 0.8, ALE-ALE, 1.7, PME-PLE, 0.3, PME-PME, 2.2, ALE-PLE 1.0.

Chelicerae. Porrect with prodorsal and lateral bands of long fine hairs. Slight ridge parallels upper cheliceral face. Rastellum a line of 10 short conical spines, not on mound, on edge above fang.

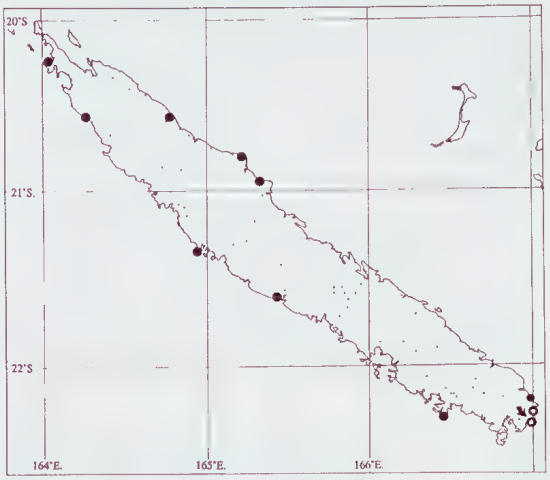

FIG. 10. Presence ● and absence ○ of *Idioctis ferrophila* sp.nov. at coastal localities sampled in New Caledonia.

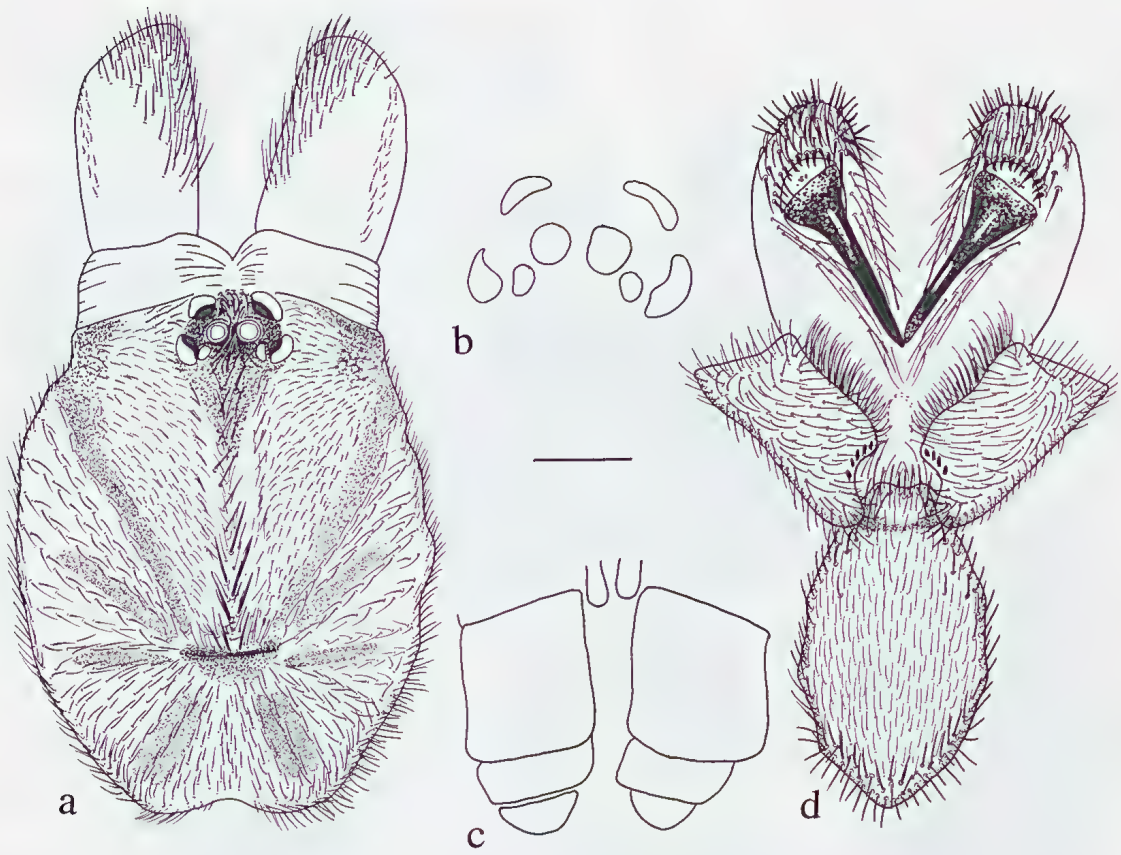

FIG. 11. *Idioctis ferrophila* sp.nov., holotype ♀. a, cephalothorax and chelicerae, dorsal view. b, eyes, dorsal view. c, spinnerets, ventral view. d, sternum, maxillae, and labium, ventral view. Scale line = 1mm (a, d), 0.5mm (b, c).

Furrow promargin with 7 thick teeth, basomesally with 1 minute and three small teeth.

Labium. 0.88 wide, 0.44 long. Labiosternal suture a narrow groove.

Maxillae. 1.52 long in front, 2.16 long behind, 1.04 wide; with c.4-6 cuspules on inner edge. Heel distinct; anterior lobe, indistinct.

Sternum. 2.80 long, 1.88 wide. With slightly darker and thicker hairs on margin; otherwise fine grey hairs medially. Sigilla shallow, indistinct.

Legs. Formula 4123. I, II thicker than III, IV.

TABLE 3. Leg measurements of *Idioctis ferrophila*, holotype ♀

	I	II	III	IV	Palp
Femur	2.88	2.68	2.08	3.08	2.24
Patella	2.40	2.16	1.52	2.24	1.68
Tibia	2.08	2.04	1.36	3.28	1.36
Metatarsus	1.60	1.52	1.36	2.44	
Tarsus	1.12	1.12	0.80	0.88	1.44
Total	10.08	9.52	7.12	11.92	6.72

Covered with fine grey hairs mixed with black setae; fine 'furry' grey hairs form narrow band near trichobothria on tibiae and metatarsi. Metatarsi I, II with distinct darker pair of setae distoventrally. Thorn spines: c.30 on prolateral patellae III, c.11 small on proximal prodorsal patella IV.

Scopula. Metatarsi and tarsi I, II, full, entire but not obscuring cuticle and separate hairs distinct. Metatarsi: III, one wide band prolaterally, ventrally and retrolaterally with setae and spines; IV, absent. Tarsi: III, full, parted by band 6-8 setal rows wide; IV, only small cluster in proximal proventral corner.

Spines. True spines only ventrally on palpal tibiae and distal metatarsi III, IV; 6-8 thicker setae on dorsal femora. Leg 1, 2: none except tibia v2 (w) and v4, respectively. Leg 3: thorn spines plus, ti v6 (w), me v8 on distal edge plus 1 thick and 4 thinner medially. Leg 4: thorn spines plus, tibia v7

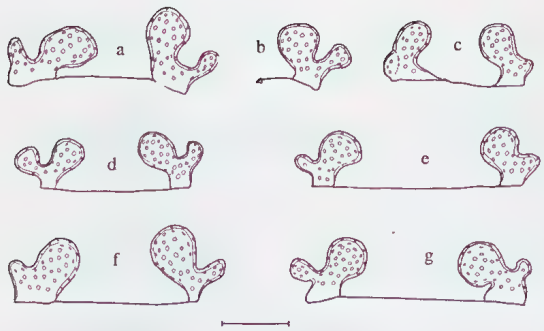

FIG. 12. *Idioctis ferrophila* sp.nov., dorsal view of spermathecae of ♀♀. a, S7211. b, S12513. c, S12517. d, S12511. e, S12512. f, S13538. g, S13537. Scale line = 0.25mm.

(w); me, v8 distal (4 close enough to be almost a comb) and 3 thinner proximad. Palp, ti v5.

Claws. 5 short (leg I) to 3 (leg IV) teeth on paired claws, palpal claw bare. Tufts dense, not enclosing claws, divided.

Trichobothria. In 2 rows, each of c.6 for 3/4 of length of tibiae; c.6-7 in short diagonal row on metatarsi; 5 clavate and c.14 filiform on tarsi in two triangular bands. Trichobothria associated with fine grey hairs.

Spermathecae. Two, each with two lobes, medial lobe broad, lateral lobe small digitiform.

Spinnerets. PMS 0.22 long, 0.08 wide, 0.08 apart, c.0.12 of basal PLS in diameter. PLS length of basal, middle, apical, and total articles = 0.76, 0.22, 0.18, 1.92, respectively.

Distribution and Habitat

Idioctis ferrophila is known from ironstone boulders on the beach at Port Boisé at the south eastern corner of New Caledonia. A trapdoor burrow with a spider like that of *Idioctis* was noted in intertidal rocks just south of Goro, 5-7 km east of Port Boisé. The specimen was not collected. At both locations, the boulders and rocks had water around their bases at low tide.

Etymology

The specific epithet is latin derived for iron (*ferros*) and greek love (*philos*) and relates to the original collection of this species from only ironstone boulders in southern New Caledonia.

Idioctis talofa sp.nov.
(Figs 2, 13-15, Table 4)

Material Examined

Holotype: ♀, Upolu, 13°55'S, 172°45'W, close to high tide mark, Western Samoa, B. J. Marples, BMNH 1974.129.1.

Paratypes: 2♀♀, Upolu, 13°55'S, 172°45'W, close to high tide mark, Western Samoa, B. J. Marples, BMNH 1974.129.2. 14♀♀ and eggs from Nu'ulopa Islet, Western Samoa, B. J. Marples, BMNH 1974.135. 1♀, 'Samoa', 19.ii.1882, Kauf, Godeffroy collection in NHW.

Diagnosis

Spermathecae two, each consisting of two similarly sized lobes, one lobe pointed. 18-20 thorn spines on prolateral proximal corner of patella III; c.9 on patella IV; prolateral distal corner of femur IV with 2-3 short spines. 4 teeth on all paired claws. Preening combs absent. Rastellum is 11 thick curved spines in single line with bases touching.

Holotype Female

Carapace 5.00 long, 4.08 wide. Abdomen 7.17 long, 4.00 wide. Total length, 15.

Colour in alcohol. Carapace orange brown, darker on caput, legs orange brown. Abdomen dorsally pallid with purplish tinge and ventrally pallid.

Carapace. With light uniform covering of silvery brown hairs, none in striae, light bush on margins, numerous brown bristles beside 10 thick and several smaller anteromedial bristles, 6-8 thick bristles between PME, c.10 between AME. Fovea distinctly procurved; clypeus absent.

Eyes. Tubercle low, distinct. AME pigmented. Group occupies 0.35 of head-width. Three rows; front row widely separated from middle row, back row slightly procurved. Eye group front width, back width, length = 40:52:33. MOQ front width, back width, length = 24:35:19. AME:ALE:PME:

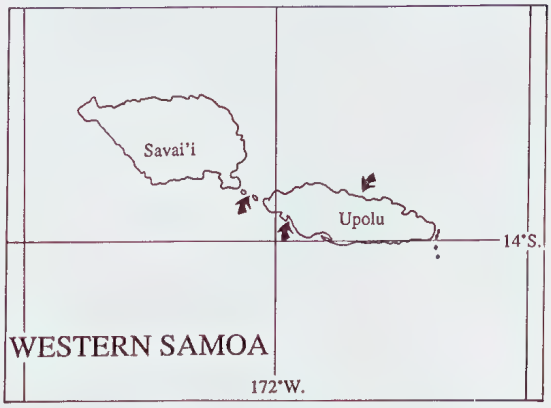

FIG. 13. Localities of *Idioctis talofa* sp.nov. in Western Samoa ➨.

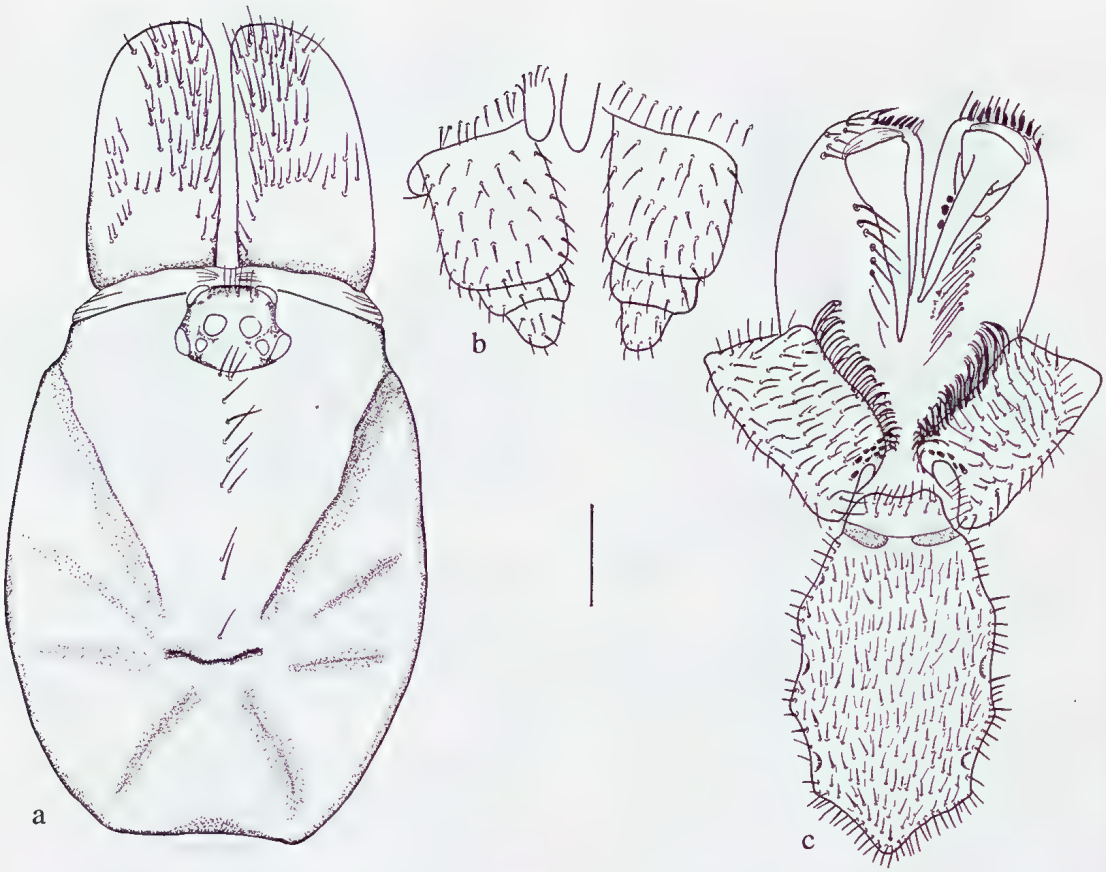

FIG. 14. *Idioctis talofa* sp.nov., holotype ♀. a, cephalothorax and chelicerae, dorsal view. b, spinnerets, ventral view. c, sternum, maxillae, labium and chelicerae, ventral view. Scale line = 1mm (a, c), 0.5mm (b).

PLE = 10:12:8:14. Interspaces: AME-AME, 0.5, AME-ALE, 1.0, ALE-ALE, 1.9, PME-PLE, 0.2, PME-PME, 2.4, ALE-PLE, 1.3.

Chelicerae. Band of moderately long brown bristles prodorsally and narrower band laterally. Rastellum is c.11 thick curved spines in single line hanging over long cheliceral edge, with bases touching. Furrow promargin with 8 teeth, all bases separate but most anterior teeth bases very close, basomesally with 6 small teeth.

Labium. 0.92 wide, 0.84 long. Separated from sternum by narrow groove.

Maxillae. 1.44 long in front, 1.96 long behind, 1.20 wide; with 5-8 pointed cuspules on inner angle. Heel rounded; anterior lobe just distinct.

Sternum. 3.24 long, 1.96 wide. Widest between coxae I. Sigilla small, marginal, indistinct.

Legs. With uniform covering of moderately long brown hairs. Scopula. Metatarsi and tarsi I, II entire, full; metatarsi III, only on proventral face; metatarsi IV absent; tarsi II with narrow band of 4-6 rows parting scopula; tarsi IV thin, short hairs, only on proventral face. Thorn spines: 18-20 on prolateral proximal corner of patella III; c.9 on patella IV; prolateral distal corner of femur IV with 2-3 short spines. Preening combs absent.

Claws. All paired claws with 4 distinct teeth; palpal claw bare. Claw tufts not enclosing claws.

Spines. No true spines dorsally or laterally except for femora and patellae III, IV. Spines on ventral legs generally weak, strong only on distal metatarsi III and IV but no so close as to form comb. Leg 1: ti p3, me 0. Leg 2: ti v3, me v1. Leg 3: pa p18, ti v6w, me v9. Leg 4, fe p3, pa p6, ti v8w, me v5 short plus 4-6 thinner. Palp: ti p1, v4.

Trichobothria. In two rows, each of c.11 for 3/4 of tibiae; c.9 in curving row on metatarsi; 3 clavate and c.15 filiform on tarsi.

Spermathecae. Two, each consisting of two similarly sized lobes, one lobe pointed.

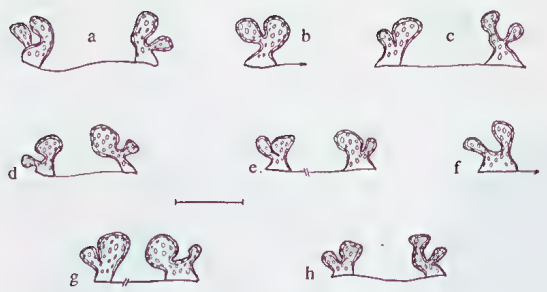

FIG. 15. *Idioctis talofa* sp.nov., dorsal view of spermathecae of ♀♀, a-h. Scale line = 0.25mm.

Spinnerets. PMS 0.36 long, 0.12 wide, bases 0.06 apart, c.0.19 of basal PLS in diameter. PLS basal, middle, apical, and total article lengths = 0.74, 0.26, 0.18, 1.18, respectively.

DISTRIBUTION AND HABITAT

Known from laval rock on beaches on the island of Upolu, and the islet of Nu'ulopa, Western Samoa (Marples, 1955).

ETYMOLOGY

The specific epithet is a Samoan word meaning 'welcome', in appreciation of the warm reception given to TBC.

REMARKS

Differs from *I. helva* in the spermathecal lobes being equal in size, anterior most teeth in cheliceral margin not fused basally, and has 1-2 thorns on prolateral distal femur IV. Of the 17 adults examined, one from 'Upolu' has only 4-6 spines on prolateral patella III of both legs. In all others, the number varies from 10-20 on a single specimen.

Idioctis marovo sp.nov.
(Figs 2, 16-18, Table 5)

MATERIAL EXAMINED

HOLOTYPE: ♀, Uepi Island, Marovo Lagoon, Western Province, Solomon Islands, Western Pacific, 8°27'S, 157°56'E, intertidal limestone beach rock, 7.vii.1990, T.B. Churchill, QM S17121.

PARATYPE: 5♀♀, same data as holotype, 7.vii.1990, T.B. Churchill, QM S17118-20, QM S17122, QM S17123.

DIAGNOSIS

Spermathecae two, each consisting of large terminally enlarged lobe with smaller one attached to the outer base of the former. Thorn spines: 25 on prolateral proximal corner of patella III; 10-16 on patella IV; prolateral distal corner of femur IV with 5 short spines. 2-4 teeth on paired claws. Rastellum of 10 strong spines in single line with bases touching. Preening combs a whorl of spines on metatarsi III, IV. ♂♂ unknown.

TABLE 4. Leg measurements of *Idioctis talofa*, holotype ♀

	I	II	III	IV	Palp
Femur	3.36	2.80	2.36	3.42	2.52
Patella	2.28	2.16	1.72	2.58	1.64
Tibia	2.12	1.96	1.64	3.17	1.36
Metatarsus	1.64	1.40	1.28	2.75	
Tarsus	0.88	1.08	0.80	1.00	1.32
Total	10.28	9.40	7.80	12.92	6.84

HOLOTYPE FEMALE

Carapace 3.92 long, 2.96 wide. Abdomen 5.28 long, 2.96 wide. Total length, 12.

Colour in alcohol. Carapace yellow brown, orange brown on caput; legs yellow brown; chelicerae red brown. Abdomen pallid but dorsally with two purple brown markings at anterior and posterior ends.

Carapace. With light uniform covering of silvery brown hairs, none in striae; light bush on margins; numerous brown bristles beside 10 thick and several smaller anteromedial bristles, 6-8 thick bristles between PME, c.10 between AME. Fovea very slightly procurved.

Eyes. Tubercle low, distinct. AME pigmented. Group occupies 0.48 of head-width. Three rows; front row widely separated from middle row, back row straight. Eye group front width, back width, length = 32:40:27 MOQ front width, back width, length = 21:27:13. AME:ALE:PME:PLE = 8:12:6:13. AME-AME, 0.8, AME-ALE, 0.9, ALE-ALE, 1.3, PME-PLE, 0.1, PME-PME, 1.9, ALE-PLE, 0.9

Chelicerae. Band of stiff silver bristles prodorsally and two narrow bands retrolaterally. Rastel-

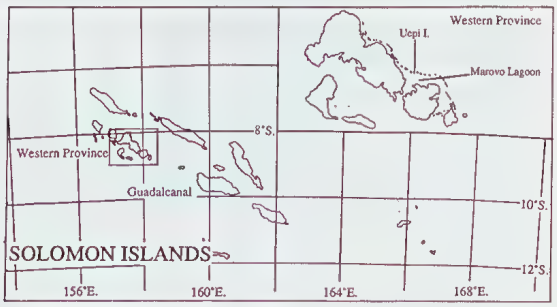

FIG. 16. Location of *Idioctis marovo* sp.nov. at Uepi Island in the Western Province (inset), Solomon Is.

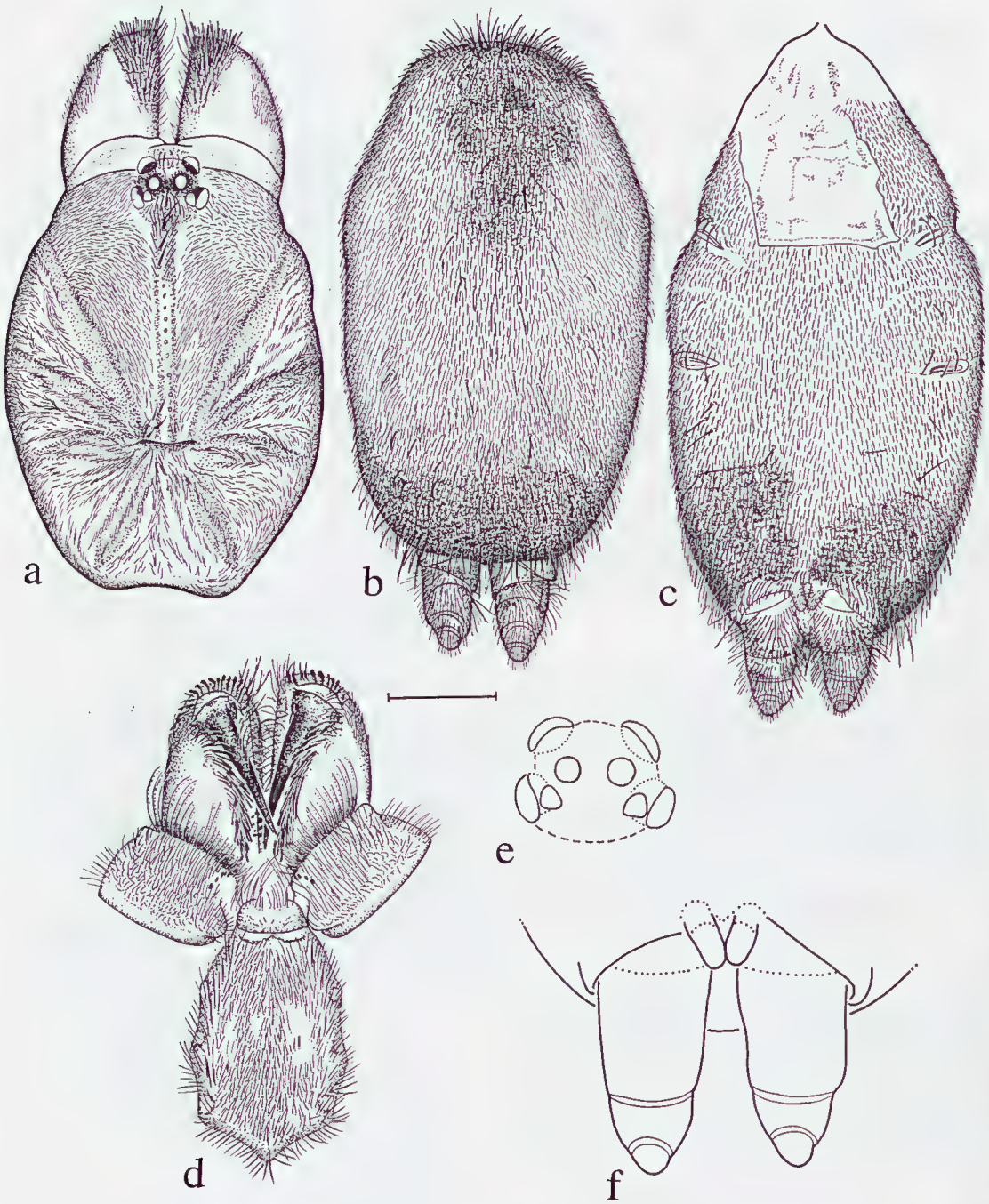

FIG. 17. *Idioctis marovo* sp.nov. holotype ♀. a, cephalothorax and chelicerae, dorsal view. b, abdomen, dorsal view. c, abdomen, ventral view. d, sternum, maxillae, labium and chelicerae ventral view. e, eyes, dorsal view. f, spinnerets, ventral view. Scale line = 1mm (a-d), 0.5mm (e, f).

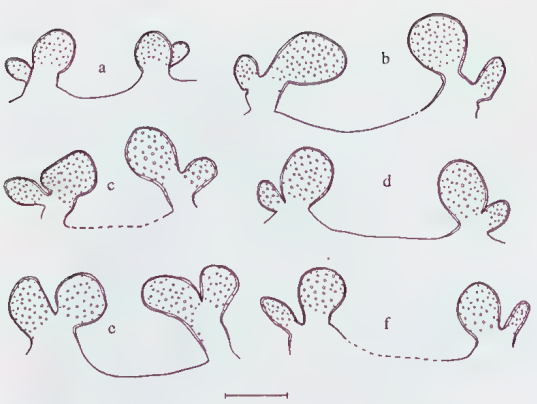

FIG. 18. *Idioctis marovo* sp.nov., dorsal view of spermathecae of ♀♀. a, S17119. b, S17123. c, S17122. d, S17121. e, S17120. f, S17118. Scale line = 0.25mm.

lum of 10 strong spines in single line with bases touching overhang cheliceral edge. Furrow promargin with 7 teeth, all bases separate but most anterior teeth bases very close, basomesally with 4 small teeth.

Labium. 0.64 wide, 0.28 long. Separated from sternum by distinct narrow groove.

Maxillae. 1.00 long in front, 1.44 long behind, 0.76 wide; with 5 pointed cuspules on inner angle. Heel rounded; anterior lobe just distinct.

Sternum. 2.24 long, 1.52 wide. Sigilla small, oval, and marginal, increasing in size posteriorly.

Legs. With uniform covering of moderately long brown hairs. Scopula: metatarsi and tarsi I, II, entire, full; metatarsi III, only on proventral face; tarsi III, with band of 4-6 rows of setae parting scopula; metatarsi and tarsi IV absent. Thorn spines: 25 on prolateral proximal corner of patella III; 10-16 on patella IV; prolateral distal corner of femur IV with 5 short spines. Preening combs a whorl of spines on metatarsi III, IV.

Spines. No true spines dorsally or laterally but 3-5 long fine black setae on femora I. Spines on ventral legs generally weak, strong only on distal metatarsi III and IV but no so close as to form comb. Leg 1: fe 0, pa 0, ti v2w, me 0. Leg 2: fe 0, pa 0, ti v2, me v1w. Leg 3: fe 0, pa p24 thorn spines, ti v2w, me v10. Leg 4: fe p5 thorn spines, pa p10-16, ti 0, me v7 in distal whorl. Palp, ti r1, v4 + 3w.

Claws. Paired claws with 2-4 distinct teeth; palpal claw bare. Claw tufts just enclosing claws.

Trichobothria. In two rows, each of c.11 for 3/4 of tibiae; c.15 in curving row that splits into two rows for the distal half on metatarsi; 6 clavate and c.16 filiform that split into two rows each two wide, two centrally and distally, on tarsi.

Spermathecae. Two, each consisting of large terminally enlarged lobe with smaller one attached to the outer base of the former.

Spinnerets. PMS 0.26 long, 0.14 wide, bases 0.06 apart, c.0.30 of basal PLS in diameter. Basal, middle, apical, and total article lengths of PLS = 0.74, 0.12, 0.14, 1.00, respectively.

TABLE 5. Leg measurements of *Idioctis marovo*, holotype ♀

	I	II	III	IV	Palp
Femur	4.88	4.64	3.60	5.12	4.16
Patella	3.28	3.12	2.48	3.60	1.84
Tibia	3.28	3.20	2.64	5.36	2.84
Metatarsus	2.56	2.32	2.40	4.16	
Tarsus	2.32	1.60	1.68	1.92	2.08
Total	16.32	14.88	12.80	20.16	10.56

Distribution and Habitat

Known from limestone beach rock and the root bases of coconut trees in the littoral zone on the island of Uepi, in the Marovo Lagoon, Western Province, Solomon Islands.

Etymology

The specific epithet is taken from Marovo Lagoon, Solomon Islands (where the spiders were collected), which has been nominated for World Heritage listing. In the face of increasing pressure from mining and logging activities, its pristine state is a credit to the wisdom of the local people.

Remarks

Females of *I. marovo* differ from those of all other species except *I. eniwetok* in that patella III is clearly shorter than tibia III, and from *I. eniwetok* in the presence of numerous thorn spines on patella IV.

Nihoa gen.nov. Raven & Churchill

Diagnosis

Nihoa can be distinguished from *Idioctis* by the wider sternum, the medially located teeth on the paired claws of ♀♀ and the absence of a second row of teeth on the claws of ♂♂. The two genera are readily distinguished by the presence of distinct pattern dorsally on the abdomen of *Nihoa*. *Nihoa* also differs from both *Idioctis* and *Idiophthalma* in the absence of a rastellum and from *Rhianodes* Raven in the absence of a groove on the anterior face of the maxillae.

Description

Carapace hirsute, without pattern. Fovea very

broad, straight to slightly procurved. Abdomen with distinct pattern or mottling. Rastellum absent. Maxillae usually with c.10-20 cuspules on inner anterior corner; anterior lobe indistinct, posterior heel produced. Labium wide, without cuspules. Sternum long, narrow (about 1.4 times longer than wide, rarely narrower), with small, marginal sigilla, if evident. Scopulae (♀ ♀) entire on metatarsi and tarsi I-III, in distal half mixed with setae on metatarsi III, and one small triangle proventrally on metatarsi IV, if present; dense and divided by narrow band of setae.

Spines (rare value in parentheses). Leg 1: femur, p0 d0-4 r0, patella, 0, tibia, p0-1 v2-7, me p0 r0-1. Leg 2: femur, p0 d0-4 r0, patella p0, tibia p0-1 v0-4, metatarsus 0 v1-2. Leg 3: femur p0-1 d0-5 r0, patella p6-30, tibia p0(2) r0(2) v0-7, metatarsus p0-3 r0-3 v0-13. Leg 4: femur p0 d0-7 r0, patella p3-16, tibia p0 d0 r0(2) v0-7, metatarsus p0-7 r0-4 v2-9.

Paired claws of ♀ ♀ with teeth on medial keel; claws of ♂ ♂ with or without one row of teeth. Tarsi with clavate and filiform trichobothria. ♂ ♂: tibia I with prolateral spur and megaspine, more distal prolateral megaspine and associated cuticular 'thumb'; palpal bulb pyriform; embolic tip flanged.

Type Species

Nihoa mahina sp.nov.

Remarks

Raven's (1988) inclusion of *Idioctis hawaiiensis* in *Idioctis* was presumably based upon the notion that it was the only genus that could be on such remote islands. He did identify that the species was the sister group of all other *Idioctis* species but lacked data on the ♂ of the type species to confirm the generic diagnosis.

Distribution and Habitat

Known from Nihoa Island in the northern group of the Leeward Islands from terrestrial habitats.

Included Species

Nihoa mahina sp.nov.Nihoa I., Leeward Islands, NW Pacific

Idioctis hawaiiensis (Raven, 1988)Necker I., Leeward Islands, NW Pacific

Nihoa mahina sp.nov. Churchill & Raven (Figs 19-22, Table 6)

Material Examined

Holotype: ♂, Nihoa I., 22°10'N, 163°10'W, Leeward Islands, northwest Pacific Ocean, 40ft.[12.2m] above sea-level, on rocks near camp in moonlight, 15.ii.1981, S. Conant, Bernice P. Bishop Museum.

Paratypes: ♀ (allotype), Nihoa I., 22°10'N, 163°10'W, Leeward Islands, Hawaii, in sleeping bag, vi.1981, S. Conant; ♀, Nihoa I., 2.ii.1981, drowned in seep pool, S. Conant; ♀, Miller Valley, Nihoa I., vi.1982; all in Bernice P. Bishop Museum.

Diagnosis

Paired claws of ♂ ♂ with teeth. Upper cuticular process on tibia I of ♂ ♂ at base of spur. Spermathecae two coniform mounds.

Holotype Male

Carapace 10.00 long, 9.67 wide. Abdomen 10.00 long, 6.83 wide. Total length, 24.

Colour in alcohol. Carapace, legs and chelicerae red brown. Abdomen dorsally yellow brown with medial longitudinal discontinuous band of brown flanked laterally by somewhat paired, brown spots anteriorly and recurved brown bands posteriorly. Abdomen ventrally yellow brown with four small brown marks almost equidistant, centrally. Sternum, maxillae, and labium red brown. Spinnerets yellow brown.

Carapace. Fine silvery hairs form uniform covering intermixed with numerous setae; line of 6 thick and several finer anteromedial bristles, and several thick bristles between ALE; striae glabrous. Fovea slightly procurved.

Eyes. Tubercle low. Group occupies 0.24 of head width. Eyes in three rows. Eye group: front width, back width, length = 71:82:60. MOQ front width, back width, length = 44:60:31. AME:ALE:PME:PLE = 16:22:16:24. Eye interspaces: AME-AME, 1.1, AME-ALE, 1.0, ALE-

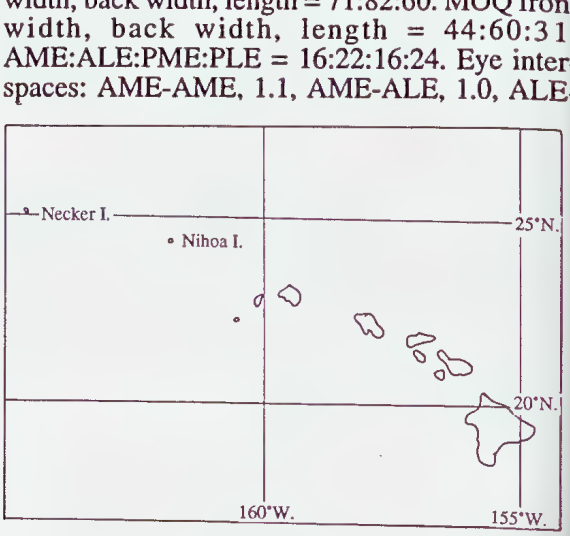

FIG. 19. Localities of *Nihoa* in the Leeward Islands. *N. mahina* sp.nov. on Nihoa I. and *N. hawaiiensis* (Raven) on Necker I.

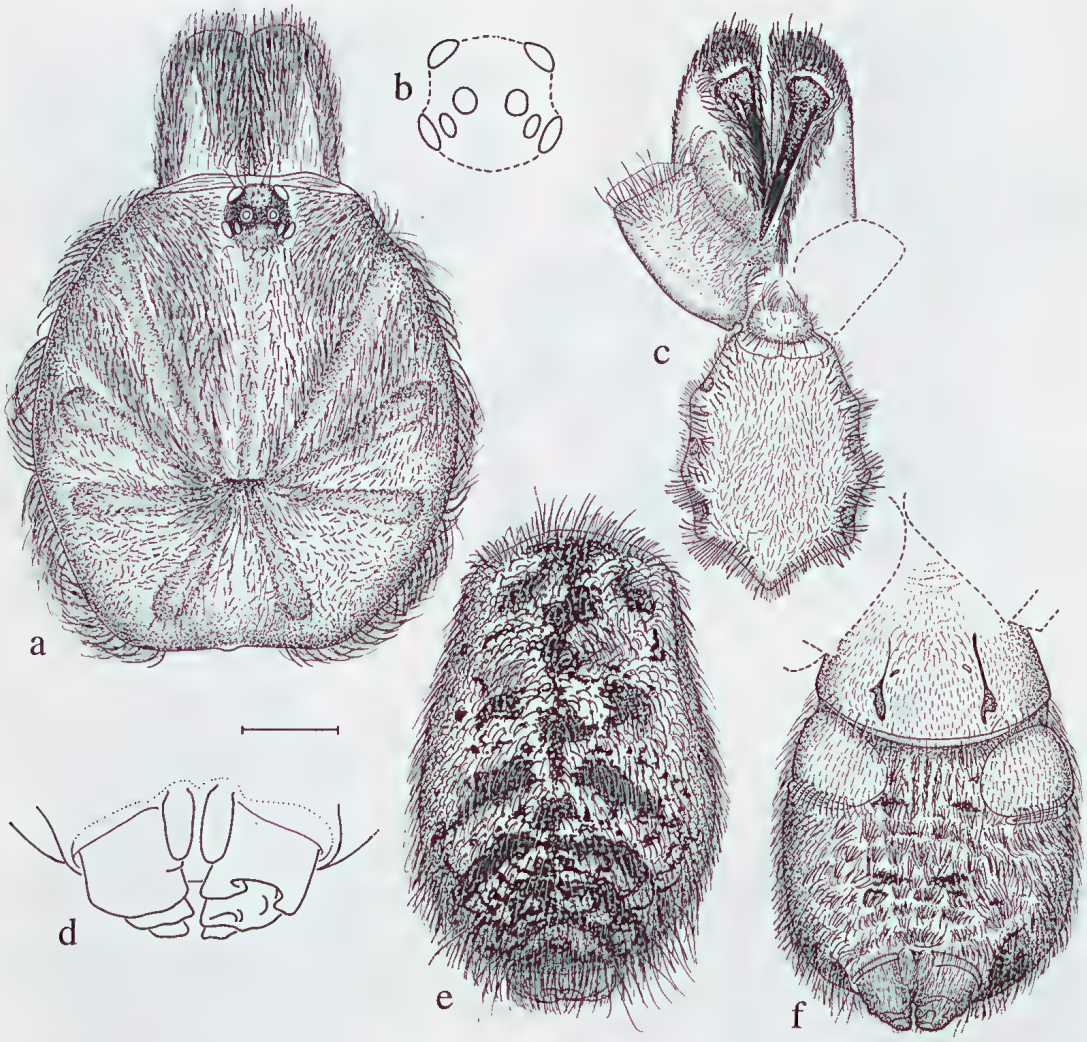

FIG. 20. *Nihoa mahina* sp.nov. holotype ♂. a, cephalothorax and chelicerae, dorsal view. b, eyes, dorsal view. c, sternum, maxilla, labium and chelicerae, ventral view. d, spinnerets, ventral view. e, abdomen, dorsal view. f, abdomen, ventral view. Scale line = 2mm (a, c, e, f), 1mm (b, d).

ALE, 2.3, PME-PLE, 0.1, PME-PME, 2.4, ALE-PLE, 1.1.

Chelicerae. With prodorsal and lateral bands of setae and fine silver hairs. Rastellum only a line of 20-25 long pointed bristles on distal edge. Furrow promargin with 8 thick teeth and 3 smaller teeth; 12 small teeth basomesally. Intercheliceral tumescence absent.

Labium. 1.76 wide, 0.72 long. Labiosternal suture a distinct groove.

Maxillae. 2.96 long in front, 3.60 long behind, 1.60 wide; with c.12 cuspules on inner edge. Heel distinct; anterior lobe indistinct.

Sternum. 5.60 long, 4.08 wide. Sigilla marginal, round, and posterior pair largest.

Legs. Formula 4123. Tibia I with distal, prolateral spur and short megaspine; base of spur with broad cuticular process below which is one (rarely two) spine. Scopulate surface of tarsi pallid.

Scopula. Leg I, full, thick, entire and undivided on metatarsi and tarsi I, II. Leg II scopula extends

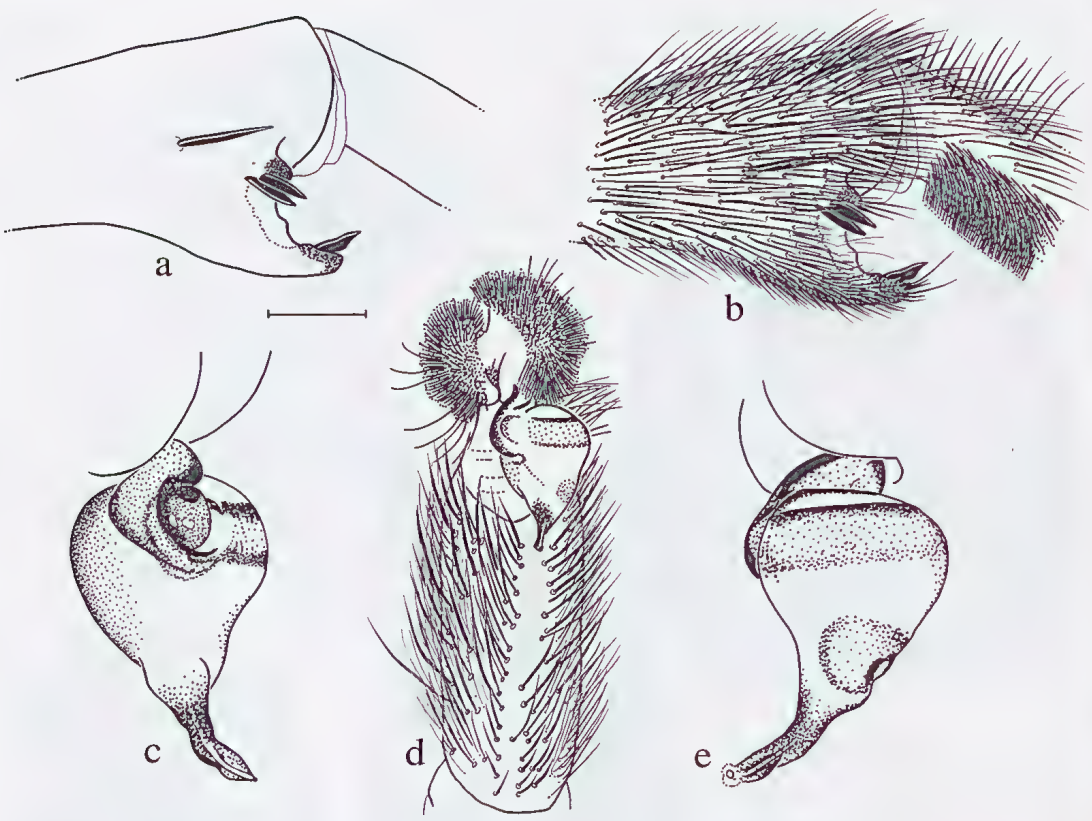

FIG. 21. *Nihoa mahina* sp.nov. holotype ♂. a, tibia I, prolateral view showing distal spur and megaspine, hair and scopula omitted. b, tibia I showing distribution of hair and scopula. c, palpal bulb. d, palpal tibia, cymbium and bulb, ventral view. e, palpal bulb. Scale line = 1mm (a, b, d), 0.5mm (c, e).

to retrolateral side; metatarsi III, thin on distal half extending to prolateral side with setae intermixed; tarsi III, entire, thick with setae intermixed; metatarsi IV, with distal prolateral 1/4 with thin scopulae; tarsus IV with setal band 2-4 rows across intermixed with thin scopulae.

Spines. Leg 1: fe p2, pa 0, ti p2+2, v3+2, me 0. Leg 2: fe p2, pa 0, ti p1, v2, me 0. Leg 3: fe p2, r3, pa 0, p2+1w, ti p2, r2, v5, me p4, r5, v10. Leg 4: fe p2, d2, r2, pa 0, ti r5, v10, me p6, r5, v17. Palp: pa 0, ti v1.

Palp. Bulb with distally flanged embolus. Cymbium with two deeply divided lobes, retrolateral face slightly convcave.

Claws. 2-4 (leg I) to 0 (leg IV) teeth in medial keel on paired claws. Tufts dense, enclosing claws.

Trichobothria. c.8 for half length of tibia, c.12 on metatarsi in single curving row; two bands each of c.4 small clavate and c.10 filiform on tarsi.

Spinnerets. PMS 0.84 long, 0.36 wide, bases 0.32 apart, c.0.33 of basal PLS in diameter. PLS basal, middle, apical, and total article lengths = 1.12, 0.64, 0.52, 2.28, respectively.

ALLOTYPE FEMALE

Carapace 10.00 long, 8.33 wide. Abdomen 10.33 long, 7.33 wide. Total length, 25.

Colour in alcohol. Carapace and legs orange brown, chelicerae red brown. Abdomen dorsally yellow brown with medial longitudinal discontinuous band of brown, flanked laterally by somewhat paired, brown spots anteriorly and recurved brown bands posteriorly. Abdomen ventrally yellow brown with four small brown marks almost equidistant, centrally. Sternum, maxillae, and labium orange brown. Spinnerets yellow brown.

Carapace. Fine silvery hairs form uniform covering intermixed with numerous setae well developed between head region and fovea; striae glabrous; fovea straight; c.30 setae between AME, c.14 between PME, c.40 long setae along medial

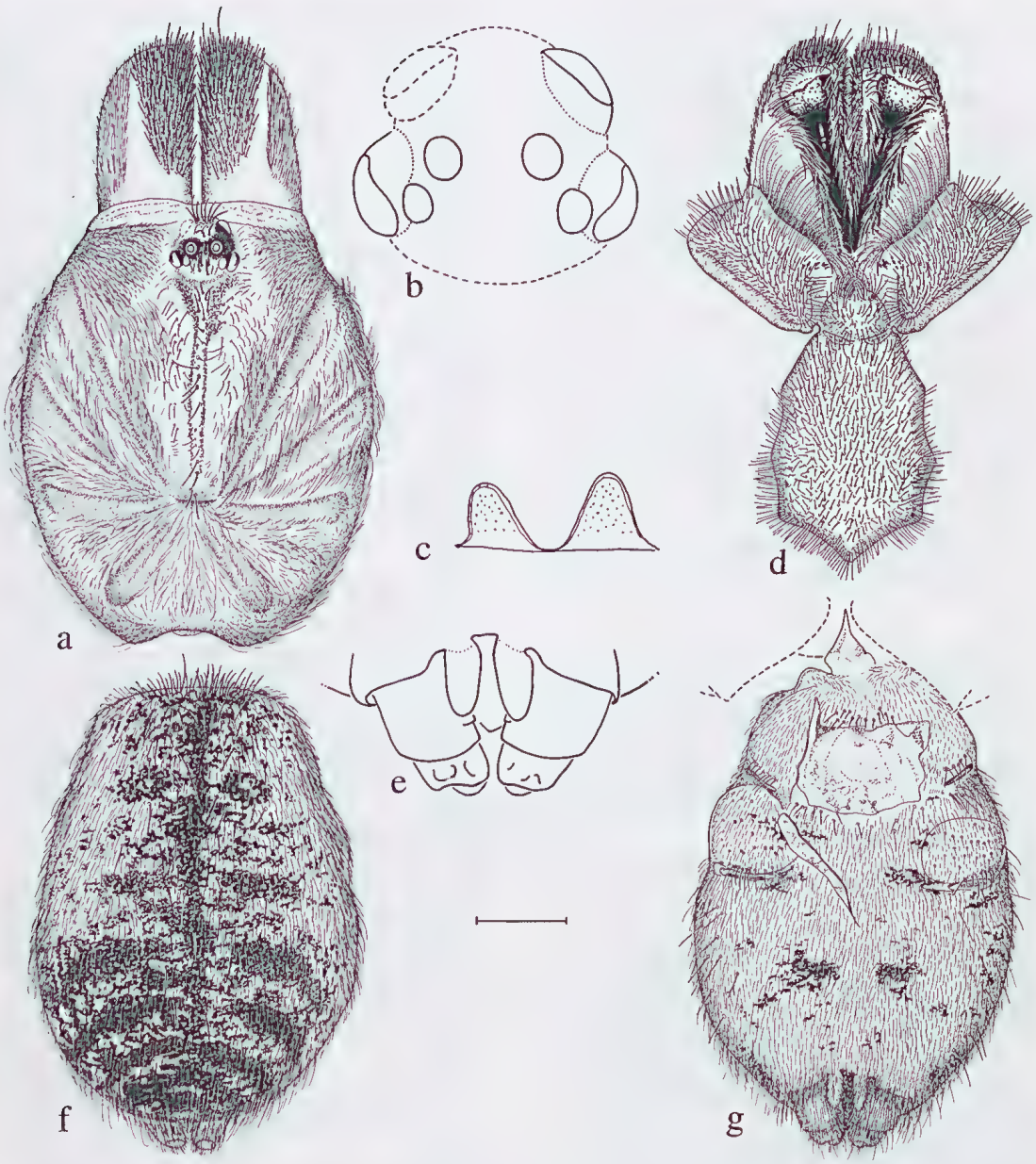

FIG. 22. *Nihoa mahina* sp.nov. paratype ♀. a, cephalothorax and chelicerae, dorsal view. b, eyes, dorsal view. c, spermathecae. d, sternum, maxillae, labium and chelicerae, ventral view. e, spinnerets, ventral view. f, abdomen, dorsal view. g, abdomen, ventral view. Scale line = 2mm (a, d, f, g), 1mm (b, e), 0.5mm (c).

caput; lateral edge of carapace with several anterior and posterior directed lines of setae with dense fine silvery hairs. Clypeus absent.

Eyes. Tubercle low. Group occupies 0.30 of head width. Eyes in three rows. Eye group front width, back width, length = 72:81:55. MOQ front width, back width, length = 45:55:35. AME:ALE:PME:PLE = 20:23:12:25. Interspaces: AME-AME, 0.4, AME-ALE, 0.8, ALE-ALE, 2.6, PME-PLE, 0.1, PME-PME, 1.8, ALE-PLE 0.8.

Chelicerae. With prodorsal and lateral bands of setae with fine silver hairs. Rastellum absent, c.35 strong bristles in line on distal edge. Furrow

TABLE 6. Leg measurements of *Nihoa mahina*, holotype ♂

	I	II	III	IV	Palp
Femur	8.33	8.16	6.16	9.50	5.50
Patella	5.33	4.83	4.83	4.83	3.16
Tibia	6.17	5.33	5.00	6.83	3.33
Metatarsus	5.83	5.66	5.33	8.00	
Tarsus	3.50	3.83	2.83	3.16	2.50
Total	29.16	27.81	24.12	32.32	14.49

promargin with 8 thick teeth and 3 smaller teeth; 6 basomesal granules.

Labium. 1.76 wide, 1.12 long. Labiosternal suture broad.

Maxillae. 2.72 long in front, 3.68 long behind, 1.60 wide; with c.10-12 cuspules on inner edge. Heel angular; anterior lobe, indistinct.

Sternum. 5.44 long, 3.76 wide. Sigilla: anterior and medial pair not evident; posterior pair small, round, marginal.

Legs. Thorn setae and preening combs absent. Tarsi broad, tarsi I c.60% of length wide; tarsi IV distally incrassate, distal width c.1.4 times basal width.

Scopula. Very dense on legs I, II: metatarsi and tarsi I, II, full, thick, entire, undivided; metatarsi III, thin on distal half with thick setae intermixed; tarsi III, entire, thick with 3-5 setae intermixed; metatarsi IV, thin in distal prolateral 1/4, divided; tarsi IV, thick, full, divided by narrow setal band 2-4 rows across and few setae intermixed, setal brush dense distally.

Spines. Leg 1, 0. Leg 2: 0, save ti p1. Leg 3: fe p2w, r2w, pa p2 thorns, ti p2, r1, v3, me p3, r3, v7. Leg 4: fe 0, pa 0, ti r1, v4, me p2, r1, v9. Palp, fe p1w, pa 0, ti p3w, v6w.

Claws. 4 (leg I) to 0 (leg IV) teeth on paired claws on medial keel. Tufts dense, just enclosing claws. Palpal claw very small, curved, bare.

Trichobothria. In two rows each of c.8 for half length of tibia; c.11 on metatarsi in single curving row; c.3-5 clavate and 12-14 filiform in each of two bands on tarsi.

Spermathecae. Two coniform mounds.

Spinnerets. PMS 0.96 long, 0.44 wide, bases 0.16 apart, c.0.53 of basal PLS in diameter. PLS basal, middle, apical, and total article lengths = 1.12, 0.44, 0.48, 2.04, respectively.

Distribution and Habitat

Known only from the island of Nihoa in the Leeward Islands, northwest of Hawaii.

Etymology

The generic name refers to the type locality. The species name is a Hawaiian word for moon, given that the type specimen was collected in the moonlight.

TABLE 7. Leg measurements of *Nihoa mahina*, allotype ♀

	I	II	III	IV	Palp
Femur	6.66	6.50	5.66	7.33	5.00
Patella	4.66	4.16	3.50	4.66	3.50
Tibia	3.83	4.00	3.33	5.50	2.66
Metatarsus	3.50	3.16	3.50	5.33	
Tarsus	2.00	2.33	1.83	2.66	3.16
Total	20.65	20.15	17.82	25.48	14.32

Remarks

Males of *N. mahina* differ from those of *N. hawaiiensis* in the presence of teeth on the claws of leg I and in the basal position of the cuticlar process on tibia I. Females differ in the coniform spermathecae, in having 4, rather than 2, teeth on the claws of leg I, and in the darker abdomen dorsally.

Nihoa hawaiiensis (Raven), new comb.
(Fig. 19)

Idioctis hawaiiensis Raven, 1988:6; Platnick, 1989:93.

Material Examined

Holotype: ♂, Necker I., Leeward Islands, north-west Pacific, 23°35'N, 164°42'W, E. H. Bryan Jr, 29.vi.1923, AMNH.

Paratype: ♀, same data as holotype, AMNH.

Other Material

The types and also from Necker I., Leeward Islands: ♂ 23.vi.1982, S. Conant; 4♀♀, Annex Hill, alt. 82m. 24.vi.1984, S. Conant; all in Bernice P. Bishop Museum, Hawaii.

Diagnosis

Paired claws of ♂♂ without teeth. Upper cuticular process on tibia I of ♂♂ prolateral, well above spur. Spermathecae two long domed mounds.

Distribution, Burrow and Habitat

The spiders were found under rocks in burrows on very sparsely vegetated hillsides on Necker Island, one of the Leeward Islands, northwest of Hawaii.

SPERMATHECAL VARIATION IN *IDIOCTIS*

This paper includes the first documentation of spermathecal variation in a genus of the family Barychelidae. Shape of spermathecae has been

used widely in mygalomorphs to distinguish between species (e.g., Schiapelli & Gerschman de Pikelin, 1962; Forster & Wilton, 1968; Raven, 1984a). As such, spermathecal shape has been considered a relatively stable and useful diagnostic character. Rarely are exceptions well supported. In his excellent and detailed revision of *Euagrus*, Coyle (1988) showed extensive variation in the shapes of spermathecae of one species, *E. mexicanus*. On the other hand, Raven (1984b, 1990) found in the *Aname maculata* group (Nemesiidae) and *Trittame* (Barychelidae), respectively, that spermathecae are almost constant within a species group. Moreover, Raven & Churchill (1991) noted that one shape is widespread in barychelid genera and may be the family synapomorphy.

Among mygalomorphs, barychelids have received little attention from taxonomists or ecologists, presumably because they build cryptic burrows. They are also under-represented in museum collections. Hence, from the limited material available variation in shape of spermathecae has been unclear but assumed to be minimal. In *Idioctis*, we find that this variation is usually too great to be useful as a specific character on its own, even though it was stable in species of *Encyocrypta* .

Recognition of a number of species in which the shape of the spermathecae cannot be diagnostic may seem unwarranted. In a major revision of Pacific barychelids (Raven & Churchill, in prep.), a plesiomorphic spermathecal shape has been identified and found to be widespread. However, as with *Idioctis*, barychelid males do show mutually exclusive differences where none were evident among their (unequivocally) conspecific females. Hence, interspecific differences can be sufficiently clarified with non-sexual somatic characters.

ACKNOWLEDGEMENTS

We sincerely dedicate this paper to Ms Julie Gallon, who assisted with the collection of *Idioctis yerlata*. Julie has been missing since 2 August, 1990, and we will continue to miss her dearly. This research, visits to European museums, and collections made in New Caledonia, Fiji, the Solomon Islands, and Singapore were funded by an Australian Research Council grant to RJR. The authors are indebted to the generous hospitality of Dr Jean Chazeau of O.R.S.T.O.M., Nouméa, New Caledonia. Ms Clare Bremner and Mrs Bronwyn Mitchell made the excellent figures 1, 8, 11, 14, 17, 20-22; RJR did the rest. We kindly thank Mr Joseph Koh, and Associate Professor Dennis Murphy of the University of Singapore, for their hospitality and assistance to RJR in acquiring comparative material of *I. littoralis*. Mr John Ravenscroft kindly assisted in the search for *Idioctis helva*, in Fiji. We are grateful to Dr G. Rack, Zoologisches Institut and Zoologisches Museum, Hamburg, for the loan of types of *Idioctis helva*, to Dr J. Gruber, Naturhistorisches Museum, Vienna, and Mr P.D. Hillyard, British Museum (Natural History), London for the loan of *Idioctis*, material from Samoa, and to Ms Sabina Swift, Bernice P. Bishop Museum, Honolulu, for sending the new material of *Nihoa*. The invitation of Dr Harry Parnaby to TBC to accompany the Australian Museum expedition to the Solomon Islands is gratefully appreciated. TBC warmly thanks the local people of the Marovo Lagoon area for their co-operation and hospitality. We are grateful to Dr S. Conant for data on habitats of *Nihoa mahina* and *Nihoa hawaiiensis* in Hawaii.

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SHIPWRECK AND HISTORICAL SURVEY: CHILCOTT ISLET, CORAL SEA

R.A. COLEMAN

Coleman, R.A. 1992 06 29: Shipwreck and historical survey: Chilcott Islet, Coral Sea. *Memoirs of the Queensland Museum* 32(1): 31-53. Brisbane. ISSN 0079-8835.

Many Coral Sea reefs appearing on modern charts were first discovered by unsuspecting sailing ships that struck the reefs and were wrecked in the 18th and 19th centuries. In 1845 the teak, India-built barque, *Coringa Packet*, was totally wrecked on a reef surrounding a small sand islet subsequently named Chilcott Islet after the ship's Captain.
In the late 1870's, Chilcott Islet was briefly mined for guano (phosphate) by F.E. Beaver & Co. of Melbourne. During 11-12 December, 1991, the author located wreckage believed to be the remains of *Coringa Packet* and conducted a brief preliminary survey. The wreck is considered to be archaeologically significant because of its potential to illustrate technical detail of a poorly-documented vessel type ('Country vessel'/Opium Clipper) and of Indian shipbuilding practice during the first half of the 19th century. □ *shipwreck, Indian shipbuilding, guano mining, archaeology, history, Coral Sea.*

R.A. Coleman, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; *14 January, 1992.*

The Coringa Islets, comprised of Chilcott Islet and South West Islet, lie respectively in 16°57'S by 150°00'E and 16°59'S by 149°53'E in the Coral Sea.

The group is named after the sailing barque *Coringa Packet*, which was wrecked there in 1845. Chilcott Islet, where the wreck actually occurred, is named after the ship's Captain, F. Biggar Chilcott.

The Coringa Islets are within the Coringa-Herald National Nature Reserve which was proclaimed under the *National Parks and Wildlife Conservation Act 1975* on 16 August, 1982. The Reserve is managed by the Australian National Parks and Wildlife Service (ANPWS).

The Queensland Museum administers the Commonwealth *Historic Shipwrecks Act 1976* in the Commonwealth Coral Sea Territory on behalf of the Department of Arts, Sport, Environment, and Territories (DASET). An essential administrative duty of the Museum, under the Act, is to locate, identify and assess the Australian maritime heritage resource and make recommendations to the Minister for its better appreciation, protection and preservation.

On the basis of archival research, it was determined that the *Coringa Packet* wreck had the potential to meet criteria for additional protective measures and warranted preliminary field investigation.

An opportunity was presented for the author and a volunteer assistant to join a multidisciplinary scientific charter organised by Dr James Charley of the Botany Department, University of New England, Armidale. Dr Charley obtained the necessary permit to conduct scientific research within the Reserve. The charter vessel, TSMV *Kanimbla* was to visit a number of reef and islet systems in the area including Lihou, Tregrosse, Diamond, Magdelaine, Coringa and Herald for a total voyage time of fourteen days.

Although it was intended to locate and examine two nineteenth century wrecksites at the eastern end of Lihou Reef, whilst there bad weather caused the abandonment of that part of the program. However, the position of a recent, unidentified wreck was noted but persistent rain squalls prohibited our approaching the site with safety. Only its two masts and central stack are visible above water and it appears to be a cargo vessel or bulk carrier of approximately 120-150m in length. The condition of the mast tops suggest that the wreck occurred within the past 10-20 years.

Whilst ashore at Turtle Islet, Lihou Reef, material was discovered on the beach near the waterline at the northern end, which may warrant an investigation of the surrounding reef when the opportunity presents itself. The material consisted of a stone (suggestive of ship's ballast), a lip fragment of a nineteenth century bottle, an unidentified small circular copper attachment plate and several small pieces of iron (which were suggestive of hoop iron from wooden casks).

Our main objective was to locate and examine the wreck of the *Coringa Packet* at Chilcott Islet. Due to the constraints of a very tight schedule, only one and one half days could be spent there, one third of which time was only partially produc-

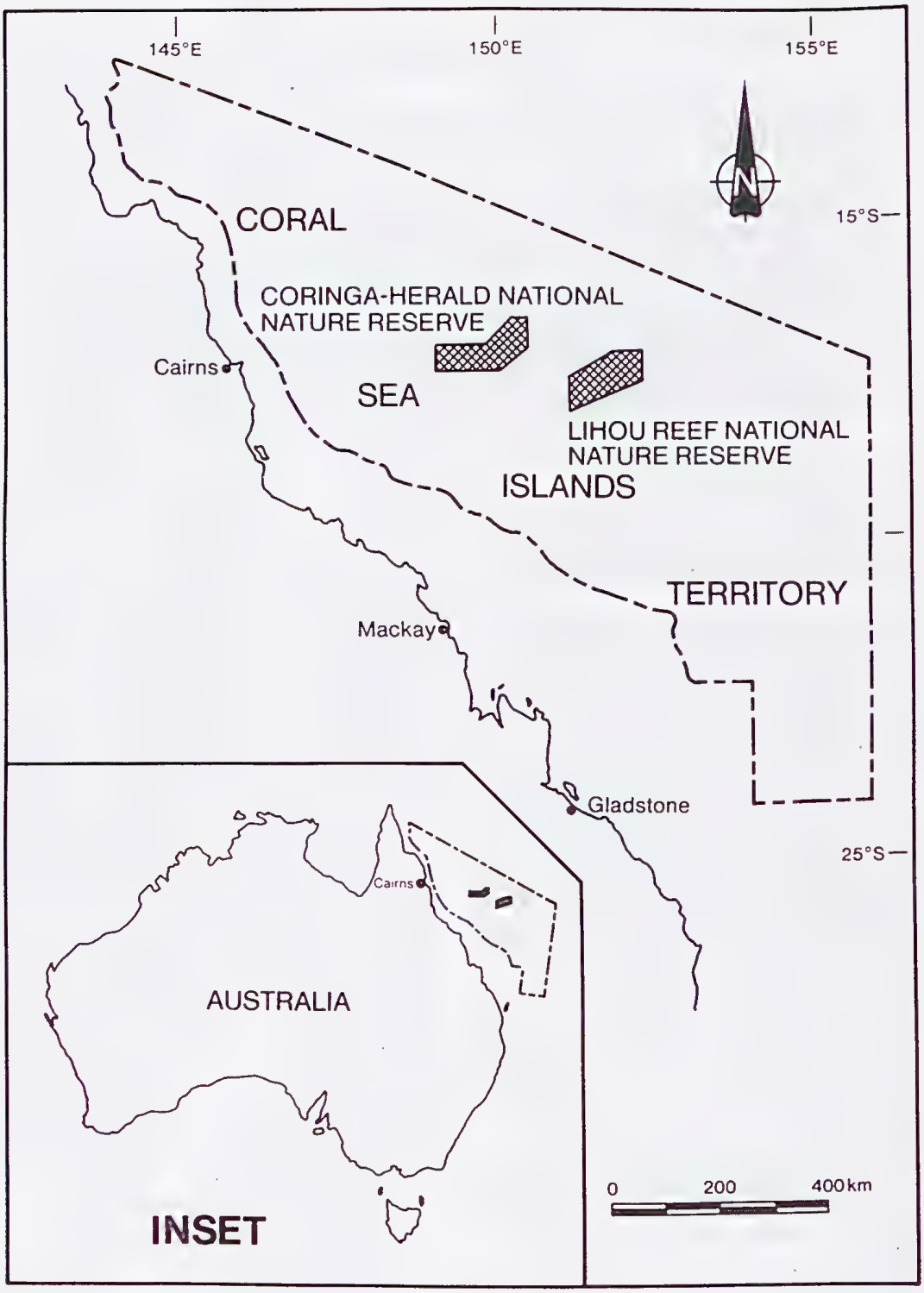

FIG. 1. Location of Coringa-Herald National Nature Reserve.

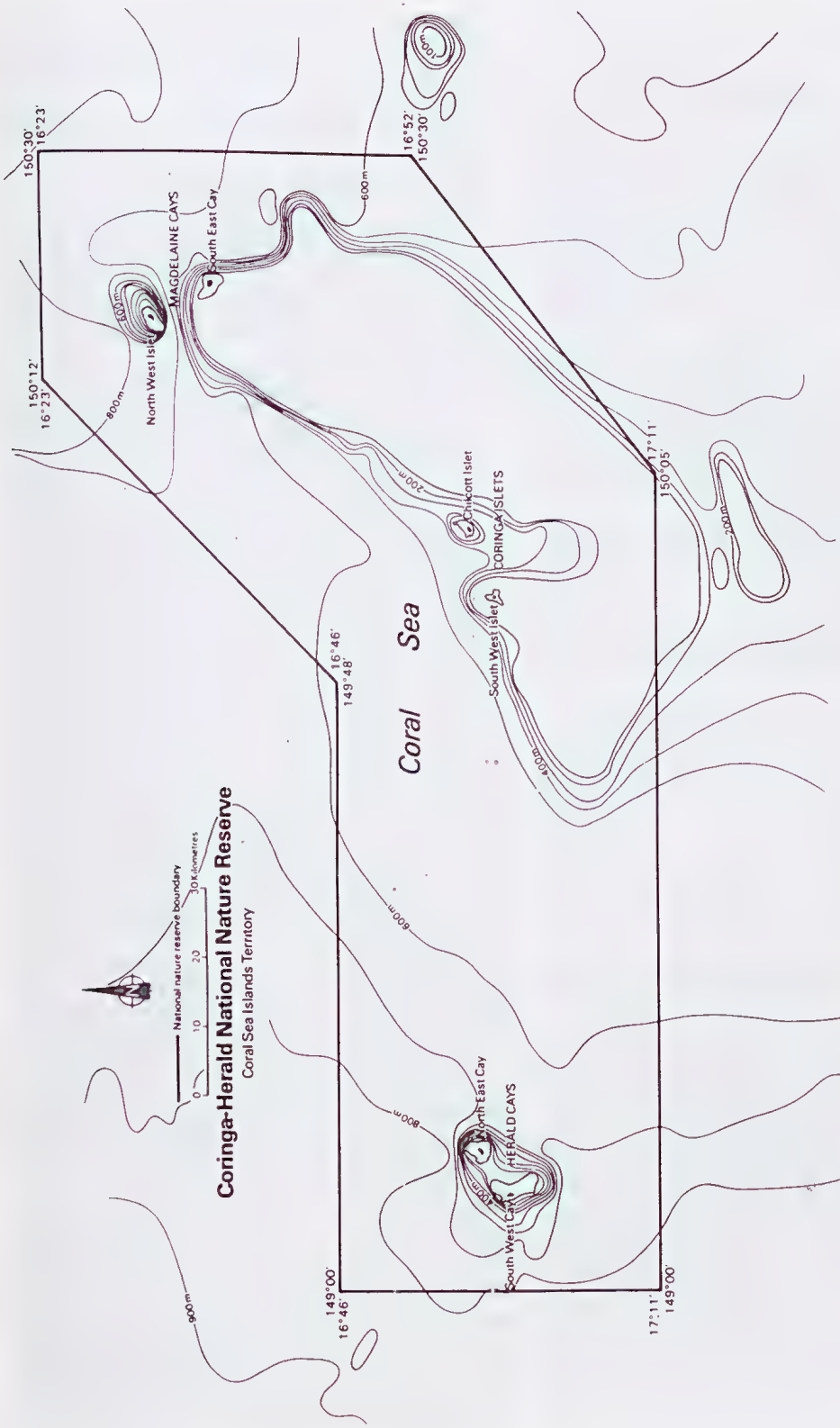

FIG. 2. Location of Coringa Islets within the Reserve.

tive due to hazardous sea conditions on the reef flat.

HISTORY OF *CORINGA PACKET*

Today, little is known of the early history of the *Coringa Packet*. However, shortly after the British Expeditionary Force was sent to resolve the opium issue in China in 1840 (an action now generally referred to as the 'Opium Wars'), she was for a period engaged in the Opium Trade. At that time she was described as being rigged as a brig.[1]

The vessel, under the command of F. Biggar Chilcott, arrived in Sydney on 11 March, 1845 and anchored off Campbell's Wharf having departed Calcutta the 11th December, Madras the 5th January, Trincomalee the 14th January, and Hobart Town the 2nd March. She carried twelve passengers and a general cargo.[2]

Advertisements in the *Sydney Morning Herald* during March, 1845 announcing her availability for cargo for Ceylon and Madras described the vessel as 'Teak Built'.

These items of information suggest that she was built and registered in India, probably Calcutta, as

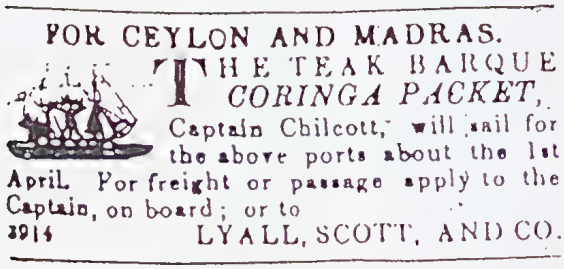
FOR CEYLON AND MADRAS.
THE TEAK BARQUE
CORINGA PACKET,
Captain Chilcott, will sail for the above ports about the 1st April. For freight or passage apply to the Captain, on board; or to
3914 LYALL, SCOTT, AND CO.

FIG. 3. Advertisement in the *Sydney Morning Herald* during March 1845

a 'Country Vessel' (India based, under European, American, or Parsee ownership: a concession begrudgingly given by the East India Company, which had earlier held the monopoly on East Indian trade.). Correspondence subsequent to her wreck, and the quantity of return cargo belonging to Chilcott, suggests that she was owned by Chilcott and possibly under charter to the Honourable East India Company as an 'Extra Ship'. This would explain why she was not listed in *Lloyd's Register*. The H.E.I. Co. maintained its own insurance. Phipps [3] lists most ships built in, and operating from, India up to 1839. He makes no mention of *Coringa Packet*, which may have been built in 1840-1.

For reasons explained later in this report, it is important to discover where the ship was built and archival research will need to continue into the problem.

When *Coringa Packet* departed Sydney bound for Ceylon and Madras with a mixed cargo and a consignment of mail on 26 April, 1845, she was listed as a 230 ton barque. Four passengers were officially recorded as being on board: Lieutenant Blackhall, Ensign Bloomfield, Mr E. Lord, and Mr Henry Van Deerlin. A large part of the crew were Indian seamen or 'Lascars' making a total complement of forty. Lyall, Scott, and Company acted as her agents in Sydney.

Chilcott, upon his arrival in Sydney, had been the bearer of correspondence addressed to the prominent pastoralists and horse breeders James and William Macarthur of Camden from their agent in Calcutta, G.A. Plaistowe and the auction house, Cockerell and Company. The Macarthurs had found a ready market for good horses among the officers of the Bengal Army and other affluent Europeans in India and had recently sent a shipment to Calcutta on the East Indiaman *Blundell*. Plaistowe reported, '...there appears a great demand for these horses, and they have been expected and talked of, three months before our arrival, and I hope they may go off well. Auction sales appear the best and most fair way of each horse attaining its value, and it is arranged that the 16th and 21st December, be the days of sale - half each day. I could sell several privately, well, but I find that would prejudice the remaining ones at auction, wherein purchasers would say the best had been taken, and the culls, only, sold publicly. I am advised, also, from Cockerell's House, to such a course.'

'Good horses will sell well here, but it is great folly in shippers sending unbroken horses. The first question I am asked here, speaking of horses - What kind of cattle? Are they broken to saddle, side-saddle, harness, double or single? I have horses that are not broken upon the Catalogue; then, they say, What a pity - you should always bring horses here, thoroughly broken, and they will meet ready sale and realise good prices.'[4]

Chilcott was not slow to realise the potential for profit and when *Coringa Packet* finally cleared Sydney Heads there were three horses on board as part of the cargo consigned under the Captain's name. His speculation may have been influenced by one of his passengers, Lieutenant Blackhall, who had been sent to Australia to investigate the potential supply of horses and other livestock to the British military in India.

What then took place is best described by Chilcott himself:

'On the 5th May, passed Wreck Reef; the wind hanging far to the eastward prevented us from weathering Alert Reef and shoals in the vicinity; bore away to the westward to clear these dangers.'

'May 7. Passed through the group of islands known by the name of Tregoss's Islands [Diamond Islets in the Tregrosse reef system]; shaped a course N.W. by W. with the intention of sighting Lizard Island, and at 9:45 P.M. while sailing at the rate of eight knots an hour, the ship struck with a tremendous crash, on a reef, and slewed broadside on; sounded the well, found seven feet water - cut away the mast and let go the anchor, for fear the ship might beat out into deep water and sink, as we could not make out anything about us but a foaming sea: the vessel continued striking violently, and the sea making a complete breach over all, and, as you may suppose, daylight was most anxiously looked for; and to our great joy, a small island or sand bank was observed to the S.W., distance about half-a-mile; (fortunately the mast had gone over the side without injury to the boats). We then rigged a pair of shears, and with great difficulty got the long boat out; all hands next employed in procuring water and provisions, and landing it on the island.'

'At night, all hands left the wreck, and slept on shore; at daylight, went again to the wreck, which we found had suffered much during the night, and got the water and provisions out; remained on the island until the 21st of May, when we then decided to man the three boats and proceed for Torres Straits, in the hope of falling in with Her Majesty's ship *Fly*, or seeking some means for the rescue of the remainder of the crew left on the island, composed of twenty-four souls. We left on the island 800 gallons of water, and provisions sufficient for four months; and I trust, ere that time expires, some measures will be taken to remove them.'

'...We had a boisterous passage in the boats, from the wreck to the Barrier Reef, and I am sorry to say, we lost the gig, which upset on the night of the 23rd, and Mr. E. Lord, passenger, was drowned; the remainder of the crew were picked up by myself and the cutter, under the charge of the chief officer.'[5]

Chilcott and his group of fourteen sailed the remaining two boats through the Barrier Reef to Booby Island, on the western side of the Torres Strait, arriving on the 31st. There, they not only found sustenance in the cave later known as the 'Post Office cave', but another group of shipwrecked people. These were the survivors of the *Hydrabad* which had been wrecked a few days earlier near Murray Island and who had arrived at Booby the day before.[6]

It was immediately obvious to Chilcott and Captain Robertson of *Hydrabad* that although a ship might be expected to call into the island at any time, the huge number of people who must survive on the limited supplies in the cave could not remain there for long. Also, Chilcott knew that to notify the authorities of his remaining crew on the islet, he must quickly convey the news to a port from which ships sailed to Sydney. Chilcott and his group were exhausted after eleven days in the boats. With a volunteer crew and several of his passengers, Captain Robertson immediately set out for Port Essington in their long boat.

In the meantime, the twenty-four Lascars left on Chilcott Islet had reached a decision. The construction of a raft from materials salvaged from the wreck had begun before Chilcott and the others had departed in the boats. Having little faith in the boats' chances of success, twenty-one of them decided to attempt to reach the mainland. They set out two days behind Chilcott, on the 23rd of May, leaving three less venturous men on the Islet.

Two days after Robertson's long boat left Booby Island, on 2nd June, the schooner *Shamrock*, Captain G. Browning, called in and took on board Chilcott and the fifty remaining survivors of the two wrecks. Their first port of call was Port Essington where, on the 7th June, they found Robertson had safely arrived. Chilcott had left letters at Booby Island for Captain Blackwood of HMS *Fly* advising of the wrecks, the survivors' progress to Port Essington, and of the situation of the Lascars left at Chilcott Islet.

The *Fly* with her small tenders *Prince George* and *Midge* had been conducting surveys off the south coast of New Guinea and had become separated from the *Midge* and the ship's second gig. Captain Blackwood dispatched the *Prince George* to Booby Island for intelligence, as that was their emergency rendezvous, and on 2 June the *Fly* weighed anchor and followed.

J. Beete Jukes, Naturalist on *Fly* recorded, 'On nearing Booby Island [on the 8th of June], we saw the appointed signal for good news flying, and found that our boats, having missed us on the coast of New Guinea, after a vain attempt to reach Caedha, or Bramble Key, had run for this little islet. We had left provisions here in the early part of the year for any ship-wrecked people that might come in their boats [the N.S.W. Government maintained supplies in the "Post Office cave"]. Availing themselves of these, and procuring a

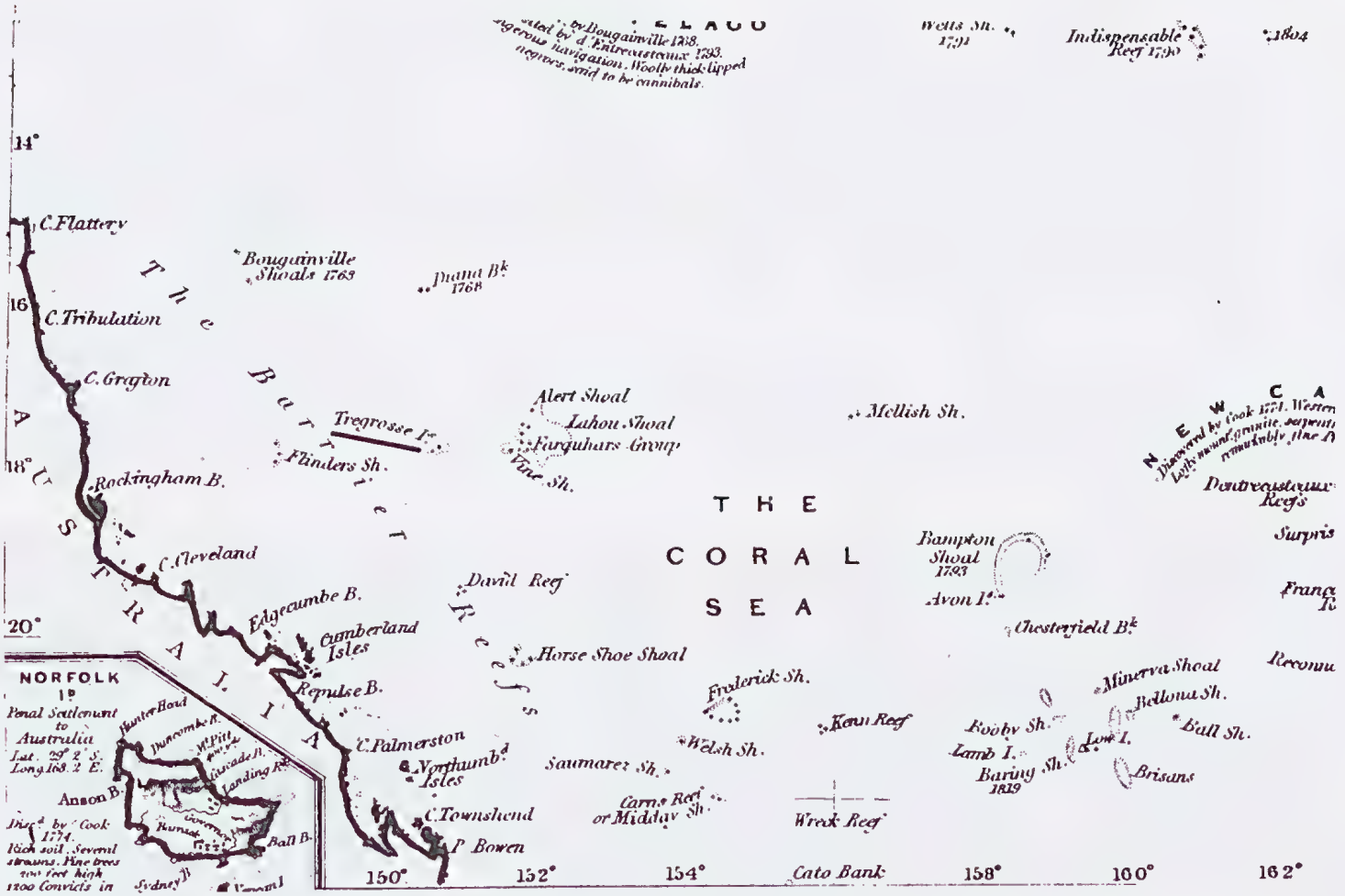

FIG. 4. Portion of a chart c.1840 published by Edward Stanford, London, and probably similar to that used by Captain Chilcott. The area immediately north and northwest of the Tregrosse Islets (underlined) would appear clear of dangers.

fresh supply of water near Port Lihou, in Endeavour Strait, [a bay on the south side of Prince of Wales Island, twelve miles to the east. The *Coringa Packet* and *Hydrabad* survivors had evidently used all the cask water in the cave. The only other water on the island is in a small rock catchment which is difficult to locate and few knew about its existence at that time], our people had left the second gig on Booby Island, and gone on in the *Midge* to Port Essington. We also found intelligence that two large vessels had been wrecked - one the *Hyderabad*, in the Cumberland Passage, near Murray Island, another the *Coringa Packet*.'

'The crews and passengers of these, consisting altogether of seventy or eighty people, had also visited Booby Island, and gone on to Port Essington, partly in their boats and partly in a small schooner [*Shamrock*] that happened to pass by. Among the passengers by the *Hyderabad* were some ladies from Van Diemen's Land, on their way to India, whose acquaintance we had had the pleasure of making when in Hobarton.'[7]

The *Fly* immediately sailed to Port Essington arriving on the 12th of June. They found that *Shamrock* had already sailed on the 10th for Ceylon with Chilcott, his mates, and two or three hands. The remaining shipwreck survivors, '...amounting to nearly 70 persons were now residing [there], and as it was impossible for the garrison to support this number much longer, and there was no probability of any other vessel touching for some months, the "*Fly*" was under the necessity of taking them to Sincapore....'[8]

Port Essington was out of the way and of no commercial interest to merchantmen coming through Torres Strait. Most sailed directly northwest from Booby Island for Coupang in Timor or through one of the Indonesian straits to Singapore.

'On the 11th of June', Captain J.B. Pain of the brig *Spy* reports, '...I took eleven of her crew [all that remained of *Coringa Packet's* Lascars who had sailed on the raft] off the nethermost [northernmost] of Sir Everard Home's Islands [at the tip of Cape Grenville], where they had been for fifteen days, subsisting on shell-fish and what little water they could find in the cavities of the rocks; three died the morning I fell in with them, and the others were in a dreadful state of exhaustion. These are the only survivors of twenty-one men who left the wreck on a raft on the 23rd of May.'[9] It would appear that a mistake in dates was made here and that the Lascars had arrived at the Home Islands on the 30th of May. According to Captain John Hews of the *Maid of Athens*, Pain picked up the surviving Lascars on the 15th of June. And Pain varies his figures in subsequent reports to say that he rescued ten, not eleven men, that eleven, not ten had died, and that they had been in the Home islands sixteen, not fifteen days.[10]

Captain Pain had been busy. On the 31st of May, he had picked up the survivors of the *Maid of Athens*, which had been wrecked, just after midnight on the 30th, southeast of Sir Charles Hardy Islands, which are a couple of miles east of Home's Islands.[11] His delay of several days in picking up the Lascars a few miles away must have been occasioned by his standing by the wreck of *Maid of Athens* to salvage what he could.

Arriving at Booby Island on the 17th of June, Pain found that Chilcott's group and the *Hydrabad* survivors had already departed for Port Essington and that *Fly* had proceeded after them. Pain left a letter at the Booby Island 'Post Office' advising of his rescue of eleven of the Lascars and the wreck of *Maid of Athens*. A copy of his letter was entrusted to the Captain of the brig *Joseph Wheeler*, then anchored at Booby enroute to Manila. *Spy* then proceeded with her passengers directly to Coupang arriving there on the 4th of July.[12] As a consequence, those at Port Essington were unaware that only three men remained at the *Coringa Packet* wreck.

Prince George, with some of the survivors on board, parted company with *Fly* at Port Essington on the 18th of June and proceeded to Sydney by the western route. The cutter arrived at Sydney on the 13th of August bringing news of the shipwrecks and the mistaken advice that twenty-four *Coringa Packet* Lascars were awaiting rescue.[13]

Governor Gipps immediately called for tenders for a vessel to proceed to the reef, '...and a schooner called the "*Frolic*" was chartered for the purpose. The Government however required that she should be commanded by a competent navigator and Mr. Yule [Commander of the survey vessel HMS *Bramble* which was at Sydney undergoing a refit] was requested to examine the candidates: the former master of her, [William Pilfold], broke down at once, and out of 6 or 7 others examined only one understood how to work out a common set of sights for time!: the owners were also very anxious for the master of the "*Frolic*" who had been a long time in their employ to continue in her, but this Mr. Yule would not consent to unless a competent "navigator" went with him, and the only one who had passed a satisfactory examination objected to go in a subordinate capacity: all this occasioned considerable

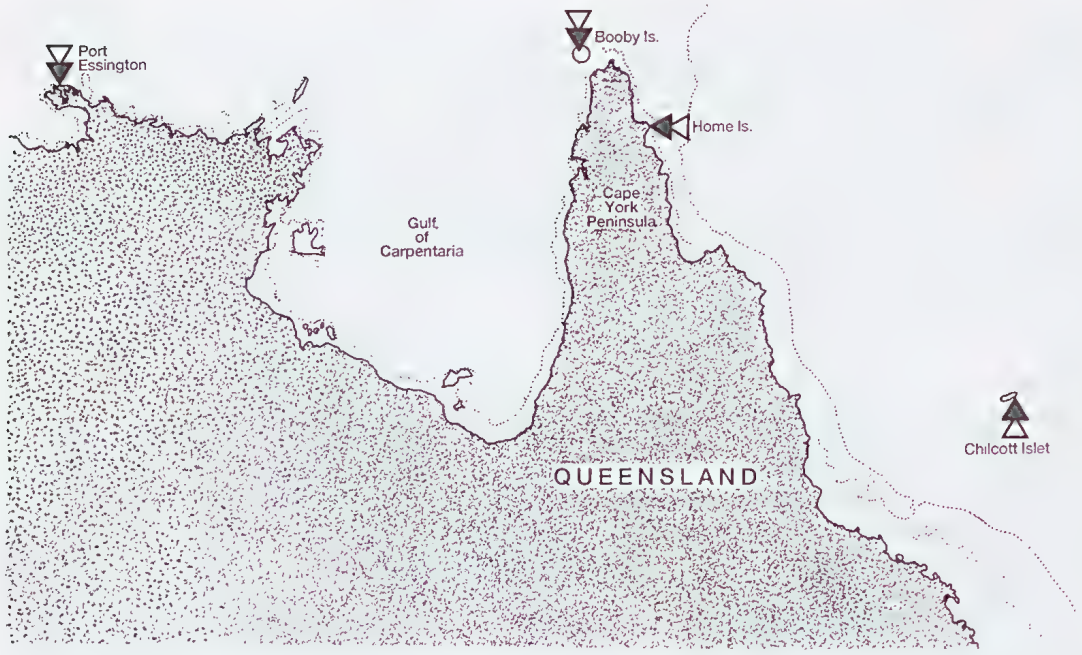

FIG. 5. Chart showing relative positions of Chilcott Islet, Home Islands, Booby Island, and Port Essington.

delay but at length a person [Mr G. Levian] was found who proved fit & willing to go as "mate & navigator" with the former Skipper and on the 19th of August the "*Frolic*" sailed.'[14]

'In the mean time however the "*Heroine*" ... whose master, McKenzie [Martin MacKenzie], a very clever enterprising little fellow had also applied, tho' in vain, for the contract, sailed for Java and in her passage touched at Chilcott's Bank [Islet] a fortnight before the "*Frolic*"....'[15] MacKenzie took the three remaining Lascars on board, dug up a chest of silver plate and other valuables which Chilcott had buried, recovered the mails, and, as was his habit, planted several coconuts so that in future, unsuspecting mariners could see the low-lying islet, before sailing on to Port Essington where (it is presumed) he lodged a claim for salvage.[16] In fact, MacKenzie was an excellent navigator and must have derived a great deal of satisfaction from having shown the bumbling bureaucrats in Sydney, and particularly Lieutenant Yule, who had insulted his sensitivities, a thing or two. He now had a double-axe to grind. Enroute to Port Essington with the men and goods he had rescued, *Heroine* struck a rock in the middle of Endeavour Strait where Yule had surveyed previously and declared free of dangers. Now who was the incompetent navigator?

Of course, the *Frolic* found no one or thing to rescue when they finally arrived at Chilcott Islet. Captain Pilfold's log book explains what took place:

'Saturday, 6th September, 1845. - At 9:30 A.M., sighted the wreck of the *Coringa Packet*, on Chilcott Island, a sand key, bearing S.W., distant three leagues. At 10:15 landed on the island (north end), and saw the place where a tent had been erected, but no trace of the shipwrecked crew. I then searched for the mails and property said to have been buried about ten paces from the tent (no parts of which were left), but I found a large hole, about that distance, in which I supposed them to have been buried; in this hole many pieces of tarpauline were strewed about, which bore the appearance of having been lately dug up, as did the hole itself. I, Mr. G. Levien [the mate], and three of my crew, then searched the island throughout, to see if we could find any letter, mark, or notice, by or through what means these men left the island; and after a fruitless search of near three hours, gave up all hope of gaining any clue of their destination, and returned on board. The *Coringa Packet* is now lying with her head to the eastward, and by all the appearances, in which I am borne out by the opinion of my crew, the copper has been stripped off on the starboard side, and the whole of the rigging, masts, and everything moveable, have been taken or carried away. There is a derrick

rigged out of the main hatchway, and the hatches all off. On the island everything valuable has been taken away; no part of the raft, spars, or casks, of any description are remaining - saving a piece of one of the lower masts [probably the one which was cut away shortly after the wreck] and an old scuttle butt, a few rags of canvas, and clothing of the crew.'[17]

Checking at the Raine Island beacon for the missing survivors, Pilfold found a letter which had been left by MacKenzie with the confusing news that *Heroine* had rescued the mails and goods but only three Lascars. *Frolic* then proceeded to Booby Island where he found Captain Pain's account of the rescue of all that remained of the twenty-one on the raft and letters explaining the others' departure for Port Essington. He then sailed on to Port Essington where he found two Lascars (one had joined the crew of *Heroine*), Chilcott's valuables, and the mail which he subsequently took on to Singapore in accordance with his charter with the New South Wales Government.[18]

Governor Gipps advised the Secretary of State, W.E. Gladstone, in a dispatch dated June 16, 1846, that he chartered the *Frolic* for £294/19/11. He had every reason to believe, he wrote, that the East India Company directors would gratefully take the charge upon themselves, and he sent Gladstone the charter documents and the details of the *Frolic*'s services; a letter from the Resident Councillor at Singapore reporting the *Frolic*'s arrival; a certificate that the men and the *Frolic*'s owners had done their work satisfactorily; and a declaration by the treasurer and auditor of New South Wales that the charter cost the N.S.W. Government £249/19/11.

The East India Company responded that it held itself accountable for £240 for the hire of the *Frolic* and considered that the balance, £54/19/11, was the value of provisions shipped on board the *Frolic* and intended for the Lascars at the wreck. But since the provisions were not applied for this purpose, but were landed at Port Essington and retained there, it was clear that the East India Company was not accountable for them. Earl Gray, who had become Secretary of State, thought that the outstanding £54/19/11 might be considered chargeable to Port Essington.[19]

SUMMARY DETAILS OF *CORINGA PACKET*

Barque
Teak built [probably India, possibly Calcutta, c.1840-41]
Tonnage - 230
Formerly engaged in Opium Trade
Copper sheathed, apparently iron-fastened,
Captain - F. Biggar Chilcott
Sydney Agents - Lyall, Scott & Company
Insurers - Apparently, H.E.I. Co.
Departed Sydney - 26 April 1845 [after a departure on 14 April aborted due to adverse winds]
Destination - Ceylon and Madras via Torres Strait
Wrecked - 7 May 1845, Chilcott Islet, Coringa Islets, Coral Sea
Cargo consigned by J.[?] B. Chilcott [was this a miss-print, or did Captain Chilcott have a relative as a partner?]
- 500 bags flour
- 30 logs cedar
- 20 kegs beef
- 1 case bird skins
- 3 horses
- 9 rams
- 30 sheep
- 25 tons coal

Cargo consigned by John Lord
- 200 bags flour

Cargo consigned by J.C. Lyall
- 12 cases cigars

Mails consisting of 249 letters for London; 400 Sydney, and 118 foreign letters, and 415 newspapers for Calcutta; 124 letters, and 152 papers for Madras; 66 letters and 102 papers for Bombay; 26 letters and 35 papers for Ceylon; 1 letter for Mauritius; and 1 letter for the Cape of Good Hope

Passengers
- Lieutenant Blackhall
- Ensign Bloomfield
- Mr E. Lord [drowned when the gig overturned]
- Mr Henry Van Deerlin [some confusion here. Francis Stewart, Chief Officer of *Hydrabad*, reported that Chilcott, two passengers, and a Miss Beech arrived at Booby Island along with eleven of the ship's hands[20]].

GUANO MINING ON CHILCOTT ISLET

I did not have the opportunity to examine the entire islet during our December 1991 visit. However, Dr Charley reported having seen two prepared blocks of guano on top of the islet near the middle of the southeastern side. The ANPWS *Coringa-Herald National Nature Reserve: Plan of Management* (p.8) briefly states, 'Relics of guano mining during the 1860's remain on Chil-

cott Islet', but does not say what the 'relics' might be. My research indicates that, officially, guano mining did not commence on Chilcott Island until 1877 and that it probably did not continue for very long.

A Mr Gilbert Carver Roberts claimed in a letter to the Earl of Derby (then British Secretary of State for Foreign Affairs), dated 9 March, 1878, that he had been the first discoverer of guano on Chilcott Island during a voyage sometime subsequent to 1871.[21]

The only official license to mine guano at Chilcott was issued to F.E. Beaver of Melbourne by a letter dated 5 February 1877. The license was for a period of seven years and cost Beaver £100. He had initially applied to mine the Willis Islets to the north. This was obviously a speculative application as he shortly afterwards wrote that he had been misinformed as to the potential of the Willis Islets and he wished to change his application to include Chilcott and the Herald Cays.[22] Obviously, he had visited the Willis Islets after his application, and prior to its approval, and had subsequently discovered a potentially richer harvest at Chilcott and the Heralds.

A story, which appeared in the *Cooktown Courier* of 28 February, 1877 entitled 'The Douglas Tragedy' and in the *Cooktown Herald* of the same date entitled 'Most Horrible Murders at Chilcot Island', gives us a graphic description of an incredible occurrence at Chilcott Islet. (Later, the *Courier* story appeared in the *Bundaberg Star* and *Burnett River Times* of 23 March, 1877 from which the following is quoted).

It is interesting to note here that Cooktown was then the centre of government administration in north Queensland due to its proximity to the Palmer goldfields. Cairns had no hospital nor newspaper and its most senior policeman was Sergeant Armstrong who submitted a report to his superior, Inspector Clohesy, at Cooktown. The *Cooktown Courier* journalist writes:

'The *Blackbird* [steamer], which arrived here on Saturday from Cairns, landed three wounded men, who were sent to the [Cook District] Hospital, and who appeared to be hacked and cut in a most terrible manner. The story they tell is one which can hardly be equaled by the most imaginative writer of fiction.'

'It appears that the *Douglas*, schooner, belonging to Messrs. F.E. Beaver and Co., of Melbourne, landed a general cargo in Cairns, and then proceeded on the 18th January to Chilot [sic] Island, lying about 200 miles due east, and worked for guano by that firm.' (Beaver had jumped the gun. He was not informed by Lord Carnarvon's Private Secretary of his successful application for a license to mine guano on Chilcott and Herald Cays until he received a letter dated 5 February 1877[23]).

'In order to obtain a favourable wind the *Douglas* went south as far as Flinders Passage, anchoring on the way under Drink [Dunk] Island, near Cardwell. While there a canoe with three blacks came off and were invited on board. They were supplied with tobacco, pipes, &c, and given to understand that they were wanted to get some companions, and to go with the vessel on her voyage. They apparently agreed, went back and brought another man. The new comer had such a disagreeable appearance that the captain refused to take him, and left with the three first. On arriving at Chilot [7 February], a small detached island, about a mile and a-half long by one broad, they found the *Alexandra*, brig, belonging to the same firm, half loaded. Mr. Beaver, one of the firm, who was on board the *Douglas*, not having enough colored labor to screen the guano fast enough, determined to go back by the *Alexandra*, half loaded as she was, and to fill up with cedar at the Daintree. The brig accordingly left on the morning of the 10th, and - the fact is worth noticing - she took nearly all the firearms of the *Douglas*, and the blacks were present when the transfer was effected.'

'That evening [actually the 14th] night fell with an over-cloudy sky, boisterous wind, and every appearance of rain. Two white men, Cochrane and McIntosh, were on shore in a hut which had been erected, and which was stored with water and rations; two of the blacks were also with them. In the early part of the night, while the white men were sitting in their hut, the blacks seemed to have killed them by simultaneous and treacherous strokes, the attitude of the bodies indicating that they could hardly have been aware of the death-stroke. Then, armed with the half axes which had served for the murder, the two blacks swam through the tempestuous sea off to the vessel.'

'No one on the schooner suspected evil, and all the whites seem to have been asleep; probably the black was waiting for his comrades. Softly they stole about their murderous work. Two white men were asleep on the deck, and both were struck so that they made no sound. One (Shaw) says that he knew nothing till he came to his senses two hours afterwards, waking in a sort of dream finding himself one mass of clotted blood, and chopped all over the head and arm. What saved him was he had wrapped a rug and thick flour bag over his

shoulders as he lay down, and the bag was dinted with the blows of the blunt axes. Thanks to the darkness of the night, he managed to crawl into the forecastle, although a black spying him as he went, aimed a blow at him, which missed. Thinking he was too far wounded to be worth troubling about, the murderers left him, and he managed to crawl aft through the hold and get into the cabin.'

'But I must go back. After the blacks had left the two men, Troy and Shaw, for dead on the deck, they went down into the hold where another sailor, Purcell, was sleeping, and attacked him. He was fearfully chopped on the face, head, and arm, one finger was cut off, and a huge gaping gash made in his back. Him they left for dead, but he subsequently crawled through the hold aft into the cabin. Meanwhile Deasy, the acting second mate, who was asleep in the forecastle, heard Purcell cry out and rushed out on deck. Never suspecting what had happened, he thought that the mooring chain had parted and shouted to that effect. In a moment he saw a blackfellow by his side with an uplifted axe over his head. He dodged the black and sung out "Captain, the blacks are murdering us." Then all rushed on him. How he escaped is a miracle. He has numerous slight flesh wounds and a severe chop on the arm, but only the most wonderful agility and pluck saved him. Once the murderers had him down on his back on the deck, and two paused to let the third get a chop at him. Even this he managed to dodge by shifting his leg, escaping with a flesh wound on the inside of the thigh. While this was going on, the mate awakened by the noise, rushed past and got into the forerigging where another man had escaped. Deasy struggled out of the grasp of the murderers and ran for the forecastle, one black following him. Getting his knife out, which up to that moment he had not been able to draw, he struck at his assailant but missed the stroke, and striking on the axe, lost his knife. Then, picking up a small grindstone lying there, he struck the black and staggered him, thus managing to get into the forecastle. A hurried search showed him there was no weapon to be found, and he came out again to make a rush for the rigging. In his haste and in the darkness, he rushed for the port side, where one of the blacks was part of the way up and another on the bulwark preparing to ascend, with the intention of attacking the mate and Lawrence on the foreyard. Deasy sprung past the black on the bulwark, and grappled the one on the rigging; but before he could wrest the axe out of his hand, the second black wounded Deasy on the heel. Finding that the next moment he would be killed, he scrambled up and reached the foreyard, when he cut blocks with the mate's knife, and the men used them as weapons to keep back the blacks, who, after a while, made no attempt to ascend.'

'During this struggle, which occupied less time than I take in writing about it, the Captain, awakened by the noise, came up, and as he laid his hand on the top of the companion, it was chopped by a blow from an axe. He retreated into the cabin, where he remained with his son, and was subsequently found by the two sorely-wounded men, Shaw and Purcell. They vainly endeavored to load a pistol, striking matches, but not daring to light a lamp. But the flowing blood clogged the pistol and damped the powder [poetic license by the *Bundaberg Star* editor, it was a revolver which fired cartridges], and they could do nothing. The steward had shut himself up in the galley; three men were on the foreyard, Deasy almost fainting, and lashed to prevent falling; and poor Troy lay on the deck near the galley.'

'There was a sort of lull. The men on the foreyard thought that all hands, except themselves, the captain, and his boy, were dead; and the blacks compelled to pause in their active attack, began to look for the bodies of their victims. Shaw, by this time, had crawled away - and, on searching the hold, they found Purcell also gone; there remained only Troy lying motionless near the galley. How long he had recovered his senses no one could tell, but he was not dead. The murderers came to where he lay, and with one blow of an axe chopped off his foot. The steward, trembling in his galley, heard the poor fellow groan, 'Oh God, I'm punished now.' Then they chopped his body and clove his head, till all life - all semblance even of humanity - was battered out of him.'

'So the terrible hours of the night wore on, and day began to dawn; the three blood-stained demons holding the deck - the steward hidden in his galley - the three men on the yard - the captain and his boy in the cabin, with the two poor wounded men weltering in their blood beside him. The grey light of morning made objects visible, and the blacks thought to finish their work. Picking up stones and pieces of coal from the hold, they began to pelt the men on the yard, who dodged the missiles as best they could. These two blacks ascended the rigging with their axes, while the third remained on deck pelting the whites. These, compelled to disregard the stones, confined themselves to keeping the axes at bay with their sling-blocks. Then the blacks found the steward was in the galley; one went to guard the companion while the other burst open the galley door. The steward

jumped through the other door, rushed to the companion, dodged the blow aimed at him by the guard, and tumbled below.'

'Now there was hope for the whites. Daylight was brightening and an un-wounded man had reached the cabin where there was a revolver and ammunition. But deliverance was not for some time. For nearly an hour the men on the foreyard had to keep at bay two of the blacks who were assailing them, while the third kept guard over the companion, cunningly shielding himself from the loaded revolver of the steward. At last an incautious movement of the guard exposed his head, and the next second a bullet went into his brain. The two blacks exchanged a hurried sentence in their own language, and one went to pick up his fallen comrade. The sailors in the foreyard dropped down the rigging. The mate first on deck took up a handspike and staggered the third man with a blow on the head, and the others closed around him. The one who had gone to the dead guard left him, saw the game was up, and jumped overboard. Two of the blacks were now dead, and the steward emptied his revolver at the third one while he swam, but did not succeed in hitting him. They saw him land on a rock, and put off in a boat after him, but he jumped again into the sea, and although they waited for him he was never seen again.'

'Then the survivors went to the Island and found the bodies of their comrades in the hut, and made sail for Cairns with the wounded. Arrived there [18 February], an inquiry was held, and the three worst wounded were sent to our hospital, where, under the skilful treatment of Dr Ahearne, a surgeon of no mean ability, they are progressing as well as could be expected.'

With minor variations, the three newspaper reports agree in the principal details.

How long after this Beaver continued his operations at Chilcott Islet is not known. The editor of the *Cooktown Herald*, with libellous gusto, first attacked the editor of the *Courier* saying that the 'niggers from Dunk Island' were his 'friends' and then accused Captain Harris of kidnapping the three natives and called for a Government inquiry. The whole sequence of unpleasant events may have prompted Beaver to forget guano mining altogether.

From what we can learn from the *Douglas* episode, at least one hut was constructed on the islet. It was furnished with a water tank and supplies, '...and arrangements made for the regular working of the deposits.' Three men, Patrick Troy, Humphrey Coghalin, and Alexander McIntosh, were buried there. Therefore, some evidence of the event may remain on the islet.

CHILCOTT'S LOCATION OF THE *CORINGA PACKET* WRECK

Captain Chilcott was quite specific as to the location of the islet and the position of the wreck. He reported, 'The position of the danger on which the *Coringa Packet* was wrecked is as follows: - Lat. 16°52'30" S., long. by the means of 20 lunar observations 149°55'45" E., the chronometer showing a longitude of 149°55' E., variation of the compass 9 degrees E.; rise of tide at springs 5 feet; the island about 10 feet above the level of the sea, surrounded by a reef dry in some places at low water, the wreck of the vessel bearing N.E. by half a mile; and the whole of this danger does not exceed 4 1/2 miles in circumference. Another small island we observed to the S.W. about four miles [South West Islet].' He also stated that the current was 'running constantly to the north-westward.'[24]

MODERN DESCRIPTION OF CHILCOTT ISLET

Australian Chart *AUS 612* (corrected to 1991) gives a position of 16°56'25"S, 149°59'55"E based upon an 'Observation Spot' at the Eastern end of the islet. Magnetic Variation 8°15'E (1984) increasing about 2' annually.

The islet is described as 'An elongated pear shaped cay with long axis oriented NE-SW. 800m long and 255m wide. Beachrock, piled up at a moderate to steep slope, fringes the S. shore line. Maximum elevation 5m ASL.'[25]

FACTORS AFFECTING SHIPWRECKS IN THE CORAL SEA

In general, isolated islands, reefs and cays obstruct the flow of water resulting in an accelerated current around the reefs and cays. Sometimes an eddy forms on the lee side. (This refers to deflection of the main, deep northwesterly current prevalent throughout the Coral Sea. The northwesterly trend of surface current, which is less affected, is still evident in the reef-top shallows and, combined with the predominant winds and seas from the southeast, generally dictate the distribution of wreck material deposited there). Over the Coral Sea Plateau, the tidal range indicated is 2m.[26]

On average, two or three cyclones per annum

affect the Western Coral Sea, usually between December and April. Although infrequent, tropical cyclones are the greatest hazard in the region. Gales occur infrequently throughout the year. Tropical depressions occur usually two or three times per year. These create conditions similar to cyclones but are less violent.[27]

THE SITES

Two separate sites were located and it is considered highly probable they are both associated with the same wreck.

SITE ONE (Chil.01)

Based upon Chilcott's description of his course,

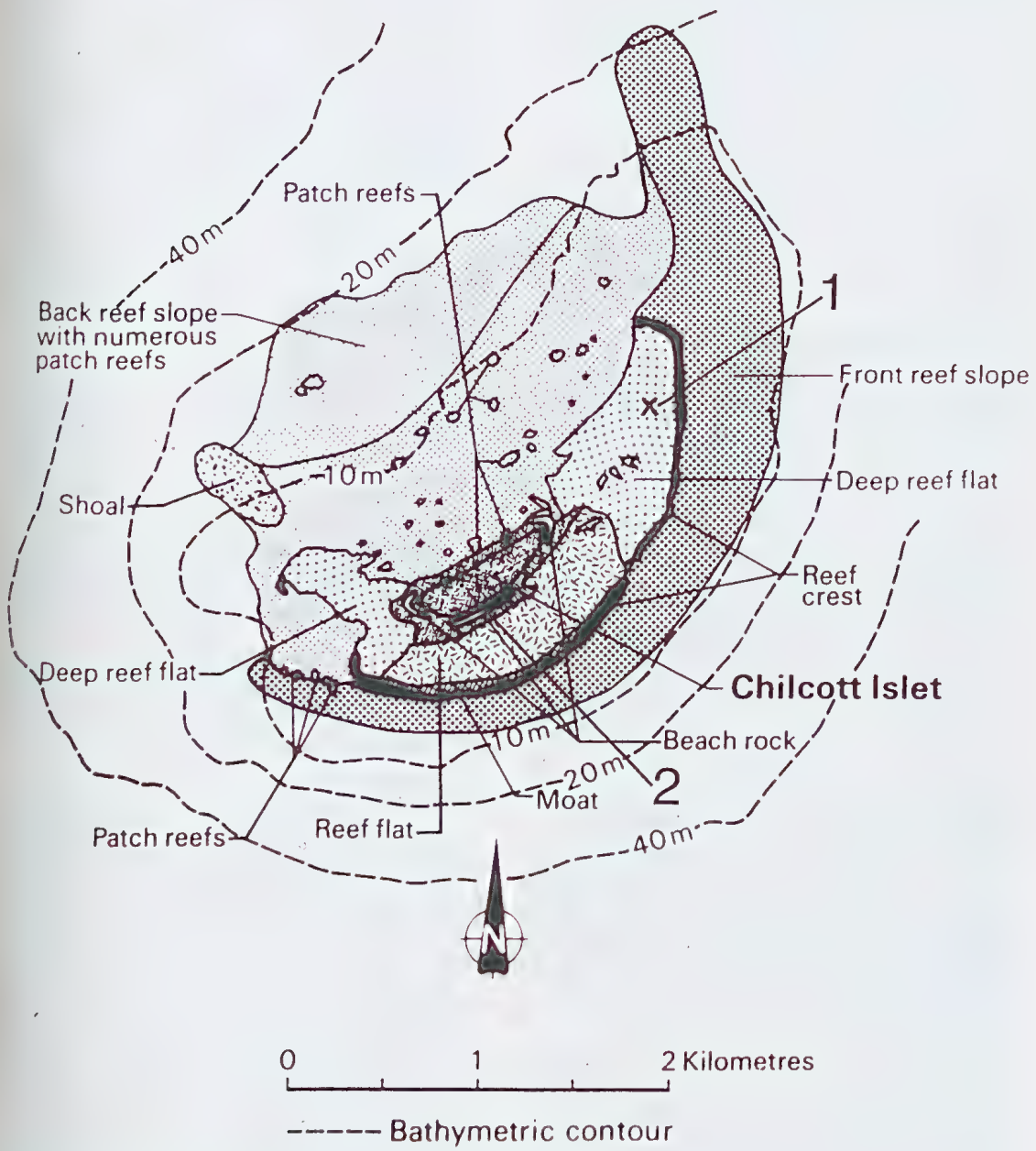

FIG. 6. Chilcott Islet. Approximate positions of sites are numbered.

(NW by W after passing through the Diamond Islets), and the position he gives for the wreck, ($^1/_2$ mile NE of the Islet), we had a good indication of where on the reef to begin our search. Our experience with other wrecks in similar situations led us to confidently expect wreck material on the reef flat scattered in a northwesterly direction from the point of initial impact.

After first exploring the beachrock at the base of the beach on the northeast point of the Islet - where miscellaneous iron remnants, a small piece of coal, and broken bottle glass were found - a 'bottle tree' was constructed on the centre of the beach facing NE as a visual reference point.

Proceeding in the zodiac onto the deep reef flat, a reciprocal back-sight was taken on the 'tree' using a monocular compass. At 225° magnetic, and approximately 30m inside the breakers on the reef crest, a reference buoy was dropped in 2m of water. Immediately, the wreck's anchor chain was seen by a diver some 10m southwest of the reference buoy.

A second flag buoy was attached to the centre of the chain and, bearing in mind the predominant winds and seas from the SE and the northwesterly direction of the current, the first buoy was transferred to the northwestern extreme of the chain to give the surface swimmers a visual reference line of potential material distribution.

The zodiac was anchored over the centre of the chain and *Kanimbla* contacted by hand-held VHF radio. The vessel recorded their own GPS position and by our holding our boat's metal fuel tank overhead as a radar beacon, they were able to record a radar range and bearing on us and the NE end of the Islet as well as its NW and SE sides. From the zodiac, magnetic compass bearings of 218° and 236° were recorded to the centre of the beach slope on the SW and NE sides of the Islet, respectively. With this information, a reasonably accurate GPS latitude and longitude of the site was calculated as 16° 55.650' S. by 150° 00.712' E.

The SE run of the chain was traced as far as the breakers would allow the divers to proceed. A pile of chain was found near that end (which then trended SSE for 7.5m before ending). The anchor deployed by Chilcott was not sighted. It should be found just off the outer edge of the reef crest amidst the breaker build-up.

The line of the chain was recorded with tapes and underwater compass. The greater length of chain lies on an alignment of 300° magnetic or 15° west of due northwest.

It being too dangerous to work on the site at high tide due to the swell and wave chop in the shallow water on the reef flat, and the timing of the lows, being at approximately 0700 and 0800 for the two mornings we had at the Islet (*Kanimbla* was to sail at 1000 the second morning), it was decided not to attempt a regimented area survey due to lack of time and trained personnel. Therefore, our swim search must be considered to be only a cursory examination of the area.

The objectives were to gain an oversight of material quantity, type, and distributional trend. Also it was intended to recover a small number of items which might assist in confirming the site as that of *Coringa Packet* and to assist in the interpretation of the material distribution sequence.

Items located included two rudder pintles (one iron, one bronze from the top of the rudder), a boom ring and goose-neck (possibly from one of the ship's gaff booms), a sandstock brick (a bed of brick was often used beneath ship's galley stoves as insulation for the wooden deck below. Galley stoves were most often placed in the forecastle area of the ship), two large rectangular dressed stones (not recovered, one measured 250×300×550mm having one end cut at an angle), two ballast stones, an iron rigging block strap with hook, a few iron fastening pins (two recovered), broken bottle glass (from base of green case bottle), an abraded piece of timber, a bob-stay plate (mounted on the stem for the attachment of the lower bowsprit brace or bob-stay[28]), a large iron thimble (used to form an eye in a bight of rope), and several unidentified iron objects (not recovered). Six short sections of studded anchor chain averaging 300mm, being loose on the reef, were also recovered for study.

The survey of Site One was curtailed by the necessity to examine and briefly record a second site discovered on the Islet itself.

SITE TWO (Chil.02)

The southeast side of the Islet (normally the weather-side) is almost entirely built of broken slabs of beachrock thrown up by cyclones. The rock extends from water level to the crest of the Islet at a height of approximately 6-8m above low water level.

Mid-way along this side, and at the top of the beachrock, storms have deposited several large ship's timbers.

The timbers are very weathered and the type of timber is not obvious from its surface appearance (although one piece, a bowsprit, has the appearance of conifer). Reference to scantling tables of the period should give us an idea of the size of ship from which they came. A sample was sub-

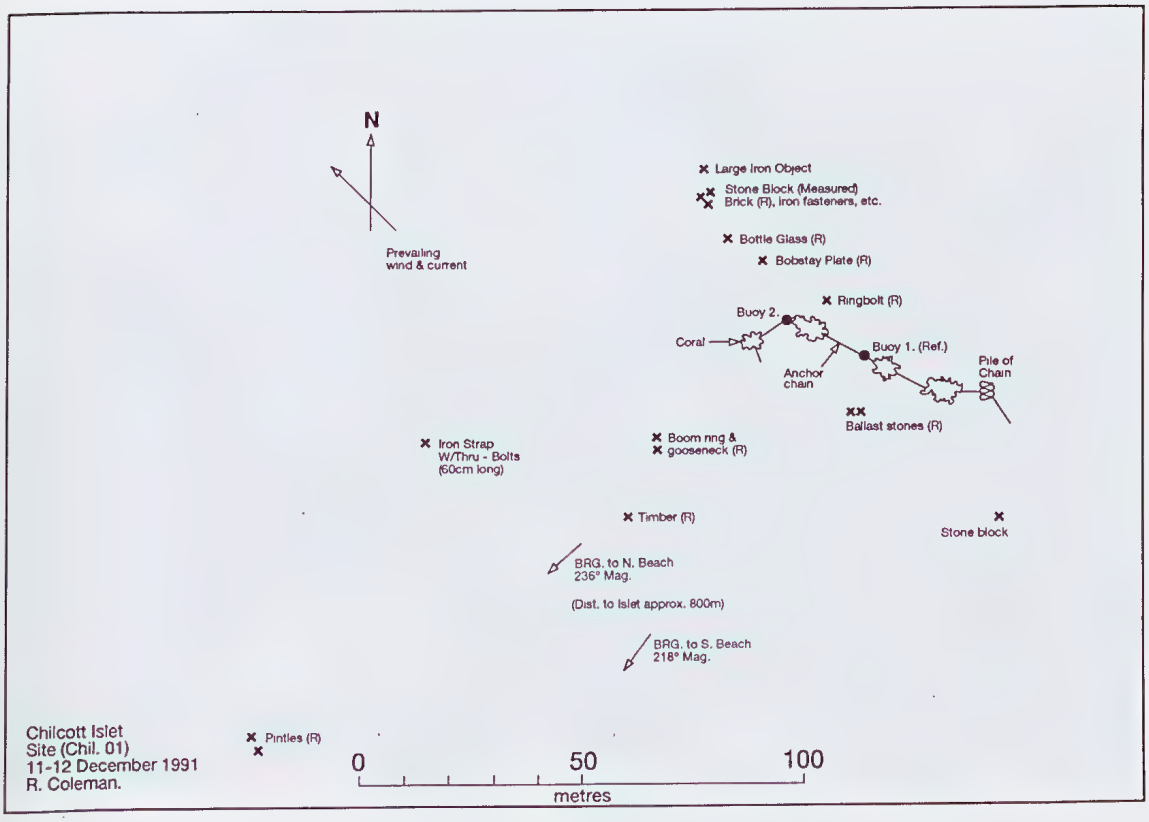

FIG. 7. Plan of Site One.

sequently submitted to the Queensland Forestry Department for positive identification of the timber species to determine where the vessel was built.

All of the material examined indicated that these were the remains of the upper bow section of a reasonable-sized vessel.

There were a number of cant futtocks and top timbers, a bowsprit, fragments of unidentified worked timbers, and a few planks, all of which had been iron-fastened.

Two iron knees (one broken) were located halfway down the beachrock and these also appear to be from the bow section as the upper arms are at an angle, or 'cant' to the flat of the lower arms. The knees were also iron-fastened.

At the water's edge, below the knees, were found two large pieces of tumbled cast iron, possibly parts of hawse pipes (through which the anchor chain passes through the ship's hull at the bow), or chain pipes (through which the anchor chain passes through the deck into the chain locker below). Other unidentified pieces of iron were observed lodged in the lower rocks.

Time did not permit precise recording. However, general measurements were taken of a few timbers and everything was photographed in situ using a photographic scale.

One top timber was recovered so that it could be accurately recorded for comparison with scantling tables and as a sample for timber identification.

DISCUSSION

It seems reasonably safe to assume that Site One is part of the *Coringa Packet*, since it was located where Chilcott said it should be and no other site was located in the general area.

Initial examination of the material from the site indicates that it is consistent with what we should expect from a vessel of *Coringa Packet*'s vintage and size. The recovered piece of timber proved to be *Tectona grandis* (teak) which is further confirmation that the site is that of the 'teak built' *Coringa Packet*.[29]

We have no record of another wreck in the Coringa Islets nor in the Tregrosse Reef/Diamond Islet complex to the southeast from which material might have floated. This lack of recorded wrecks is not to be taken as conclusive. Several ships of

FIG. 8. Site Two. Ship's timbers at top of beachrock.

FIG. 9. Site Two. Bowsprit. Length 9.4m (30feet 10inches), base dimension 38cm (1foot 3inches) square.

FIG. 10. Site Two. Iron knees.

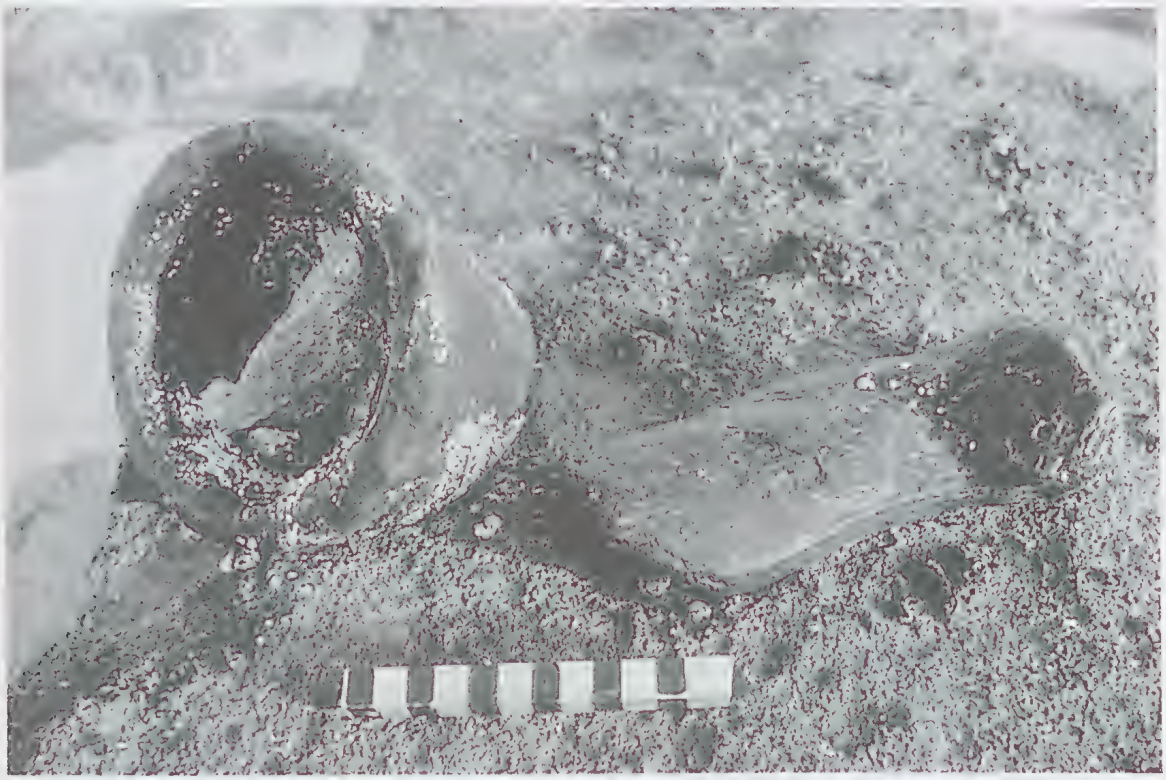

FIG. 11. Site Two. Iron objects found at water level.

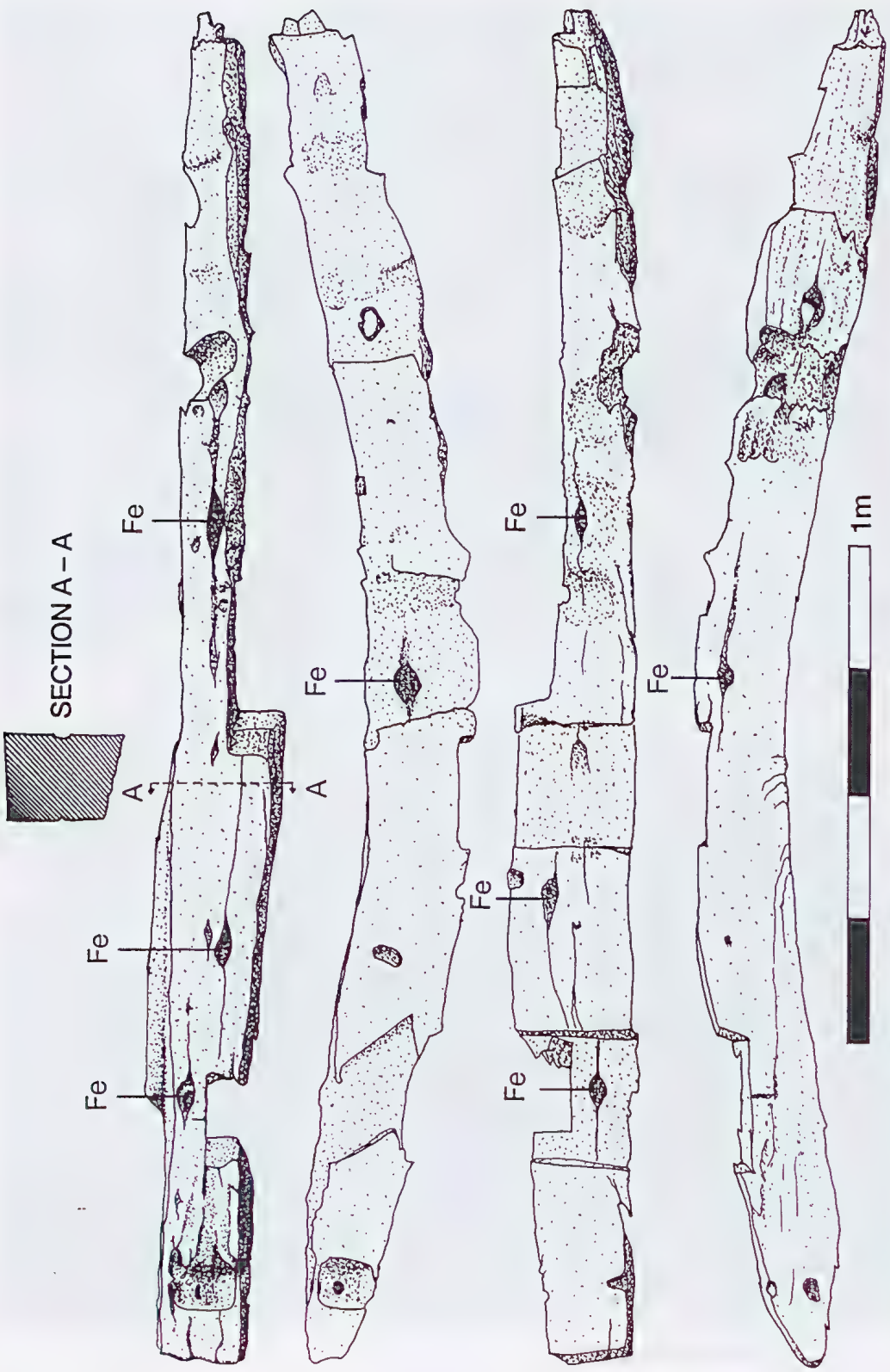

FIG. 12. Site Two. Four views and section of recovered top timber. Length 3.15m (10feet 4inches), sided 280mm (11 inches), moulded at mid-point 315mm (12.5 inches). Iron residue from fastening bolts are indicated 'Fe'.

the period were listed as 'missing' in the Coral Sea with no location given. However, although a number of India-built vessels were engaged in trade with Australia, it would be an extremely unusual coincidence to find two teak-built vessels wrecked in the same location within a few hundred metres of each other.

On first examination of the location of the material at Site Two, it is difficult, but not impossible, to reconcile as being part of the bow section of the Site One wreck.

It would be an unusual storm to carry material from Site One to the southwest and south of the Islet before it had been carried to the north beyond the Islet by winds, seas, and currents that would have generally prevailed for some months after the wreck in May. However, it should be recalled iron, glass, and coal were found on the NE tip and slightly around the north and south sides of the tip of the Islet, in a southwesterly direction from the reeftop site.

A very shallow, smooth, beachrock shelf abuts the tip of the islet extending for a radius to the east and south of some 50- 100m. In normal weather conditions the seas would be rough there. It is very unlikely that material salvaged by Chilcott or MacKenzie or building materials of the guano miners would have been brought ashore in exposed, rough shallows at that point. Rather, they would have landed just around the tip on the sheltered northern beach and opposite to the normally protected anchorage. Therefore, it is conjectured that the material found on the tip of the Islet is indeed flotsam and, at least the iron items, being of little value to any of the groups on the Islet, have been coincidentally transported there while attached to pieces of floating wreckage during a storm from the northeast.

The two rudder pintles found in the water some 200m southwest of the anchor chain are nearly identical in size having an overall length of 53cm (21 inches) and an internal breadth of c. 21cm (8+ inches). The iron pintle was the higher of the two on the rudder, iron being used above the waterline. The bronze pintle, being of similar size, was the next below and just at or below the waterline. The pin of the iron example was c. 5cm longer than that of the bronze to facilitate alignment when installing the rudder. While the overall width of the two pintles appears slightly small for a 230 ton vessel, they tell us something of the shape and style of rudder used and consequently provides some information concerning the shape and construction of the stern of the vessel. The most informative pintle dimension is that of the pin diameter (roughly measured at c. 50mm) which was the more critical in relation to the size of vessel. Steel[30] gives a recommended pin diameter of $1^{7}/_{8}$ inches (47.6mm) for vessels between 201 and 330 tons which would include *Coringa Packet* at 230 tons.

By reference to the location of the pintles on the Site One plan (Fig.7), one will see that at least the top part of the wreck's rudder, with the two uppermost pintles still affixed, became detached from the ship and floated some 200m from the site, to the southwest toward the Islet, before breaking up and a portion sinking from the weight of the metal. Generally, this would indicate that the ship was suffering a major structural break-up. The substantial timber of the rudder tiller was socketed into the upper end of the rudder post. It then passed through the stern of the ship between the large timbers of the transom framing and swung in an arc directly below the main deck beams. For the pintle pins to become disengaged from their mating gudgeons, the horizontal tiller either had to break the transom timbers, virtually destroying the stern of the ship, or snap off itself allowing the rudder to move vertically a minimum distance of 25cm (the length of the pin of the iron, or uppermost pintle). This, combined with the presence of ballast stones and the dressed stone blocks in the immediate vicinity of the stretched anchor chain indicates that the ship was coming apart where it was held by the anchor and chain. Therefore, the odds in favour of the upper bow section, which due to the absence of heavy objects was reasonably buoyant, floating to the southwest and eventually being thrown up on the rocks before it could float to the northwest beyond the islet, are greatly improved.

Again referring to the Site One plan, one will observe that the lie of the majority of chain is SE-NW as is the axis of the majority of loose material. Chilcott states that when the ship struck, she '...slewed broadside on....'[31] There can be little doubt that her head had come about from her sailing course of northwest by west to the northeast and she was then port side to the reef, the edge of which runs to the northeast at that point. Chilcott then cut away the mainmast to lighten ship and to reduce windage and the pendulum effect and dropped an anchor. He says the sea was '...making a breach over all.' Swinging to the anchor at the dictates of the southeast wind and sea and the current from the same direction, and grounding in the shallows of the reef, the ship, for a time rested (according to Pilfold's observations four months after the wreck) with her head to the east. Pilfold's reference to the copper being

removed from her starboard side indicates that she was then heeled onto her port bilges making it difficult to remove copper from that side.[32]

A possible explanation of subsequent events is that, in time, spring tides and associated swells may have lifted her sufficiently for the ship to swing her head to the southeast and her stern to the northwest thus aligning the anchor chain in that direction and allowing time for a concentration of heavy material to be deposited to the northwest of the chain. The chain may have parted (which would explain the jumbled pile of chain at the SE end) and the resultant tremendous force upon the forward-mounted windlass may have contributed to the upper section of bow, or at least pieces of it, being wrenched from the weakened hull. As the remainder of the hull was eventually carried to the northwest, the last of the chain dribbled from the below decks chain locker.

The top timber recovered from Site Two has been identified as *Tectona grandis* (teak).[33]

As it seems that the timbers at Site Two do date from 1845, it is remarkable that the guano miners in the 1870's, who were renown wreck scavengers, had not used them for firewood or to construct their hut and facilities. Perhaps they had an abundant supply of smaller firewood and lighter plank that required less effort to gather. Or, did Beaver & Co. abandon guano mining on the island after the *Douglas* massacre thus occupying the Islet only too briefly to cause much disturbance?

No copper alloy fastenings were observed on either site, which is an unusual coincidence in the case of nineteenth century wrecks; nor for that matter, were any metal sheathing or tacks, which are generally encountered.

The country vessel, *Valetta* (1825), excavated by the author in 1983, was iron fastened but copper sheathed over timber sheathing. Faith in the resistance of teak to the ravages of *Teredo navalis*, plus the fact that almost all metalwork used in Indian shipbuilding was imported from England or Europe[34] (and thus expensive), would seem to have justified the economies of less expensive iron fasteners and the cheaper expediency of using teak sheathing to insulate the iron fasteners from the electrolytic effect of the copper sheet. Phipps made a number of references to India-built vessels being sheathed with copper sheet over teak sheathing boards and implied that copper fastening of country vessels was an exceptional and expensive luxury.

Also, the suggestion is, that 'country' skippers and owners were quite happy with teak sheathing alone. But, in order to procure cargoes from merchants accustomed to the security of their cargo being carried in the generally dry, copper sheathed European-built vessels, they had to make the concession. Captain Pilfold of the *Frolic* pointedly stated that the copper sheathing from the starboard side of the *Coringa Packet* had been removed by the time he arrived. (Obviously by MacKenzie who seems to have salvaged everything possible[35]). Pilfold, by citing witnesses, was ensuring that he would not be accused of breaking his contract by keeping salvaged material for his own profit.

The use of conifer or other straight, reasonably clear softwood for masts and spars, including bowsprits, was normal practice in all shipbuilding. Indeed, pine spars from New Zealand and Australia were a frequent export cargo of northbound ships of the period. However, Phipps[36] states that at least the lower masts and large spars, including the bowsprit, of country vessels were frequently made of teak and sometimes 'poon' from Malacca, the upper masts and lighter spars being made from imported European, American, or Chinese pine.

The identification of the timber of the 'top timber' (the uppermost section of a frame or rib), being an internal structural member, is certainly more conclusive as to the ship's origin. Country vessels' frames were almost always made of either Sissoo (*Dalbergia sissoo* Roxb.) or Saul (*Shorea robusta* Roxb.) both of which were obtained from the forests north of the Ganges.[37] However, Phipps also mentions that, as those timbers became less available in the late 1830's, more vessels were built entirely of teak (*Tectona grandis*).

From the small amount of dimensional data collected on the Site Two timbers and the size and form of the bowsprit (including the unusual manner in which it was stepped), it would seem that the ship was designed to carry an enormous amount of sail (the relatively large crew carried by *Coringa Packet* may lend support to this theory). The rather fine stern indicated by the slightly narrow breadth of the rudder pintles (which reflects the width of the sternpost) also suggests that the ship was built for speed. These were not common features of the ordinary country vessel where speed was sacrificed for cargo volume. Rather, they were essential features of 'Opium Clippers' whose cargo took up less space. Their speed allowed them to make two or more annual round trips to China to the ordinary country vessel's one. Speed was also necessary to avoid Chinese government war-junks wishing to stop

FIG. 13. The Calcutta-built Opium Clipper *Waterwitch* with an exceptionally long bowsprit, jib-boom, and tall, raked masts allowing a tremendous amount of sail to be set.[40]

the illegal trade or pirates attracted either by the valuable opium on the outward voyage or the large amount of specie carried on the return voyage. For this reason, opium clippers were heavily armed.

A high percentage of opium clippers built in India were constructed at Calcutta. Phipps[38] lists seven being built there between 1830 and 1839. Lubbock claims that three were built at Bombay and a half-dozen at Moulmein. Essentially they were built to either of two designs. The first was a copy of a very famous American privateer. The second was specially designed for the trade by Sir Robert Seppings, the Surveyor of the Royal Navy. These were generally barque rigged. Of those built at Moulmein, only one was to the Seppings design. The others were copies of fast Mediterranean 'fruit' schooners.[39] If Phipps' or Lubbock's figures are anywhere near accurate, it can be seen that purpose- built opium clippers were a rare breed indeed.

It is obvious that Site One does not represent the primary site of a wreck. Rather, it is a loose trail of scattered, isolated material. One would expect a concentration of copper sheathing, ballast, coal, and other heavy material such as spare anchors, rudder gudgeons, etc. to be evident. Although it seems that MacKenzie salvaged everything he could from the wreck, it is predicted that much more material will be found to the northwest in the deeper water, (say, 10m), off the back of the deep reef flat where it was carried by floating portions of the ship's hull. Some material, associated with the bow section, may be found to the southwest along the southern shore of the islet.

There are three possible scenarios:

1. Both Sites One and Two are part of the same wreck.
2. Site Two is material from a wreck which floated to Chilcott from elsewhere.
3. Another wreck has occurred on Chilcott reef further to the south and opposite the Islet in an area which was not investigated.

However, it would appear that the presence of *Tectona grandis* at both sites is too consequential to ignore and that the first scenario must be the favoured option.

In the short term, further study of the material and data already collected may resolve a number of questions, but much more remains to be learned from the sites. In the interim, it is important that these preliminary findings be brought to notice and I would strongly recommend that future

private, tourist and scientific visitors and the Royal Australian Navy (frequent visitors) be advised against indiscriminate disturbance of any material remains in the Reserve unless they are conducting authorised archaeological research.

From an archaeological standpoint, there is no question that the *Coringa Packet* wreck and the guano mining aspect of the islet demand further investigation.

Whilst it is difficult to envisage the practical long-term preservation of the timbers and other material of Site Two in situ, it is critical to the study of 'country vessels' that they be precisely recorded and sampled. With this data, it may be possible to reconstruct a portion of the bow section using computer graphics, which will provide us with hitherto unknown details of an even rarer ship style, the 'Country-built Opium Clipper'. Therefore, it is recommended that, **at the first opportunity**, the material at Site Two be mapped and then, as a matter of expediency and economics, removed to a safe place where they can be studied at leisure. It is estimated that an archaeologist with a team of five volunteers assisting could accomplish this in two days if working during the northwest monsoonal period (say, late November-December). Considerable care would have to be exercised in the removal of the timbers because many of them are extremely fragile and vital information may be lost if they are damaged in transport.

In future, a controlled survey of the reef flat, and the discovery and recording of the primary underwater site, may contribute greatly to the meagre information currently known.

It is likely that a recommendation will be made to the Federal Minister, DASET, that, after consultation with ANPWS, a Protected Zone similar to the one at Porpoise Cay (Wreck Reef) be declared under the Commonwealth *Historic Shipwrecks Act 1976*. This would allow protective and management measures, specific to the nature of the resources, to be put into place.

Possible justifications for the declaration of a Protected Zone are as follows:

1. Little is known about the design or construction techniques employed in 'country vessels.' This type of ship played an important role in early Australian maritime history. Moreover, if *Coringa Packet* proves to have been built to one of the rare 'Opium Clipper' designs (of which only a few were built immediately prior to the introduction of steam, iron hulls and thus prior to the consequent decline of Indian shipbuilding) - and the chances are excellent that she was - then the recording and study of her remains are even more important.

2. Historical aspects of both the *Coringa Packet* story and that of the guano miners are of sufficient significance to warrant closer study. The material remains of both episodes can contribute to the interpretation and appreciation of these aspects. Their contribution would be in a physical sense as a part of the Reserve's resources, and in an academic sense as part of Australian and East Indian maritime history.

3. The remains are cultural heritage resources located within an administered Reserve which already has some management mechanisms in place. These unique resources require additional protective and management regimens specific to their nature.

4. Site Two, which has considerable potential to provide new information, is extremely vulnerable to natural attrition and unwitting, casual destruction or disturbance by visitors to the Reserve.

ACKNOWLEDGEMENTS

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ANOMALOPUS PLUTO INGRAM, A POORLY KNOWN SKINK FROM CAPE YORK PENINSULA.

Memoirs of the Queensland Museum 32(1): 54:- The taxon *Anomalopus pluto* Ingram, 1977, a limbless, fossorial skink was based on a specimen collected at McDonnell crossing, Cockatoo Ck, 115km S of Bamaga, Cape York Peninsula (11°33'S, 142°26'E) on 14 July, 1975. Since that time, the species has been encountered infrequently.

In 1980, an Australian Museum (AM) party collected 6 specimens on 16-17 July (AM R94360, McDonnell Ck Crossing, 1 km E of main N/S Peninsula road, 11°33'S, 142°27'E; AMR94361-2, R94484-5, R112004, 15km E of Heathlands settlement on Captain Billy Ck road, 11°45'S, 142°41'E). Eleven years later, 4 specimens of *A. pluto* were collected by officers from the Queensland National Parks and Wildlife Service (QNPWS).One specimen was collected on 6 September on the road edge during road reconstruction, c.12km E of Heathlands ranger base (11°40'06"S, 142°45'30"E). Two days later, 8 to 10 specimens were uncovered in a 30m^2 area at Eliot Ck (11°24'40"S, 142°24'43"E) during earth moving activities. Of these, only the three least damaged specimens were collected. In December 1991, QNPWS (Far Northern Region) approached the Queensland Museum (QM) to assess the Eliot Ck *A. pluto* site, an area of proposed redevelopment. I visited Eliot Ck on 18 January 1992 but found no *A. pluto*. However, four specimens were recorded from 3 other localities: 500m W of Heathlands ranger base (11°45'S,. 142° 35'E), QMJ54050 (17 Jan.), 54082 (19 Jan.); 1km E of Heathlands ranger base (11° 45'S, 142°36'E), QMJ54083, 54213 (19 Jan.); Captain Billy Ck road, 28.25 km from Heathlands ranger base (11°39'S, 142°44'E) (24 Jan.), one seen but not collected.

Habitats

Ingram (1977) recorded QMJ26261 (the holotype) under leaf litter in a small patch of monsoon forest. AMR94360, from 1 km E of the type locality, was found under a piece of wood on the verge of the road bordering a 'vine and scrub thicket' (Greer & Cogger, 1985). Rainforest communities at the type locality are small, isolated patches on grey loamy sand, surrounded by tall open forest dominated by *Eucalyptus tetrodonta* (David Jones, pers. comm.). AMR94361-2, R94484-5 and R112004 were found in low dense heath on white sand: one beneath a lignotuber and the others from a pile of debris beside a track (Greer & Cogger, 1985). The three QNPWS specimens from Eliot Ck came from tall open forest of mainly bloodwood, stringy barks, *Xanthostemon xerophylus*, acacias, scattered livistona palms and pandanus, ironwood with a grassy understory and a moderate scattering of shrubs (Mike Provic, pers. comm.). These were within a few metres of a large termite mound in powdery grey sand. The fourth QNPWS specimen came from thick heath on red/yellow powdery sand in *Melaleuca viridiflora*; *Banksia dentata*; jacksonias; acacias and xanthorrhoeas scrub (Mike Provic, pers. comm.) with abundant large red termite mounds. QMJ54040 and J54082 were collected in a stand of epacrid scrub (*Leucopogon* sp.), 100m from a small stream, from grey loamy-sand beneath a small termite ridden log which supported an active termite mound. QMJ54083, J54213 were in a similar situation but the logs, while termite-ridden, did not support active termite mounds. The specimen from Captain Billy road was in notophyll vine forest (David Jones, pers. comm.) on grey loamy-sand, in association with a termite-ridden log supporting an active termite mound.

Overall, there appears to be no corelation of vegetation types at collection sites. However, *A. pluto* has always been found in sandy substrates.

Notes

A. pluto is known from 15 preserved specimens in the collections of the QM (5), AM (6) and QNPWS (4). These are from 7 localities, all within the Heathlands area of Cape York Peninsula. Following Thomas & McDonald's (1989) classification, McDonald et al. (1991) assigned *A. pluto* a ranking of 3K because of its limited distribution and the lack of information. However, *A. pluto* localities are within a range of less than 100 km; thus, according to their criteria, a rank of 2K is correct. While it is impossible to assess abundance of *A. pluto*, the many specimens encountered at Eliot Ck suggests that it may be common in areas of favourable habitat.

Little information is available on diet. Stomach contents of QMJ54083 contained only termite fragments, not surprising from the close association between *A. pluto* and active termite nests at several localities. Absence of sand particles in the stomach of QMJ54083 may suggest this specimen had been feeding on termites within their burrows (E. Dahms, pers. comm.). Whether *A. pluto* is a specialist termite feeder or a more general feeder is unknown.

A. pluto has an elongate right lung and no right oviduct. Other lizards that have lost the right oviduct produce a brood size of one and *A. pluto* should also follow this pattern (Greer, 1989).

Tissues from QMJ54213 are deposited in the Evolutionary Biology unit, South Australian Museum.

The work was done with a grant from the Royal Geographical Society of Queensland. Kate Couper, Wayne Longmore, Paul Feeney, Martin Cohen, Steve Williams and Trevor McLeod assisted in the field. Ross Sadlier supplied details of Australian Museum specimens. David Jones, Allen Greer and Mike Provic gave helpful advice.

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P.J. Couper, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 20 *February, 1992.*

A NEW SPECIES OF SKINK OF *LERISTA* FROM QUEENSLAND AND A RE-APPRAISAL OF *L. ALLANAE* (LONGMAN).

PATRICK J. COUPER AND GLEN J. INGRAM

Couper, P.J. & Ingram, G.J. 1992 06 29: A new species of skink of *Lerista* from Queensland and a re-appraisal of *L. allanae* (Longman). *Memoirs of the Queensland Museum* 32(1): 55-59. Brisbane. ISSN 0079-8835.

L. colliveri sp.nov. is found in NE and Central Queensland. It has been confused with *L. allanae* (Longman) but, besides the strickingly different colour-pattern, it can be readily distinguished by the presence of a nubbin for a foreleg whereas *L. allanae* has no forelegs. With *L. colliveri* separated from *L. allanae*, the range of the latter species is even more restricted than thought. This rare species has only been found between Clermont and Capella, Central Queensland, within the area 22°50-23°06'S and 147°38-147°54'E. It apparently has not been met with since 1960.□*Scincidae, Lerista allanae, Lerista colliveri, new species, Queensland.*

Patrick J. Couper and Glen J. Ingram, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 14 February, 1992.

The status of *Lerista* was clarified by Greer (1967, 1986). Since 1972, the species of the genus have received much attention in the central and western States because of the work of Glen Storr (see Wilson & Knowles, 1988, for references). In that time, however, the species of Queensland have not been as intensely studied.

For Queensland, Storr (1972) clarified the status of *L. muelleri* (Fischer) and Cogger (1975) noted 9 species of *Lerista* from the State. Greer (1979) described a new species *L. ameles* from NE Queensland and Cogger et al. (1983) listed the synonymies for all species. Greer et al. (1983) added three new species - *L. cinerea, L. storri* and *L. vittata* - from NW, NE and Central Queensland and Storr (1986) erected *L. aericeps aericeps* nov., from SW Queensland and the Northern Territory.

In 1988, Wilson & Knowles reviewed all Australian terrestrial reptiles and noted 15 species of *Lerista* from Queensland. However, in 1990, Greer said *L. aericeps aericeps* Storr was a junior synonym of *L. xanthura* Storr. Even so, Storr (1991a) was unconvinced and preferred to retain *L. aericeps* as a valid species. Storr (1991b) also disagreed with Greer's (1990) and Wilson & Knowles's (1988) concept of *L. orientalis* (de Vis); he divided the taxon into three allopatric species, two of which were new: *L. zonulata* and *L. ingrami.*

Recently, Covacevich & Couper (1991b) listed 17 species from Queensland and also provided maps (1991a) of 15 of the species that were represented in the Queensland Museum collection. In this paper, we add a further new species from NE and Central Queensland that has been confused with *L. allanae* (Longman). We also re-appraise the status of the rare skink, *L. allanae.*

Measurements are in millimetres. Specimens prefixed by J are housed in the Queensland Museum, by R are in the Australian Museum. Queensland regions follow Ingram & Raven (1991).

Lerista colliveri sp.nov.
(Figs 1-3)

Lerista allanae Wilson and Knowles, 1988: 291, photo no.523; Cogger, 1983, 1986: pl.672; Covacevich & Couper, 1991a: fig.305

MATERIAL EXAMINED

HOLOTYPE: J16181 Hughenden (20°51'S, 144°12'E), CQ, J. Devecchi.

PARATYPES: J33128 Battery Stn (19°26'S, 145°51'E), NEQ; J33123 Harvey Ra, Mingela (19°41'S, 146°20'E), NEQ, A. Taplin, Mar 1979; J33124 Fanning R Stn, c.1.5 km from hsd (19°44'S, 146°26'E), NEQ, K.R. McDonald, F. Parker, 1 Mar 1980; J33127 Fanning R Stn, 1.5km from hsd (19°44'S, 146°26'E), NEQ, K.R. McDonald, F. Parker, 1 Mar 1980; J46266-7 Mingela Ra, Fanning R Stn (19°44'S, 146°27'E), NEQ, K.R. McDonald, F. Parker, 1 Mar 1980; R62452 Red Falls at the Basalt Wall, 60km due WNW Charters Towers (19°56'S, 145°44E'), NEQ, E. Cameron, H. Cogger, A. Greer and P. Webber, 16 Jul 1977; R113515-39 area in and near Basalt Wall in vicinity of Reed Falls, Lolworth Ck, (19°56'S, 145°44E') CQ, A.E. Greer, E.N. Arnold, D. Kent, R. Sadlier, G. Shea, 10-12 Sep 1984; J33125-6 Toomba Stn (19°58'S, 145°34'E), NEQ, B.C. Lawrie, D. Locke, 1 Jun 1981; J45648 Dun-

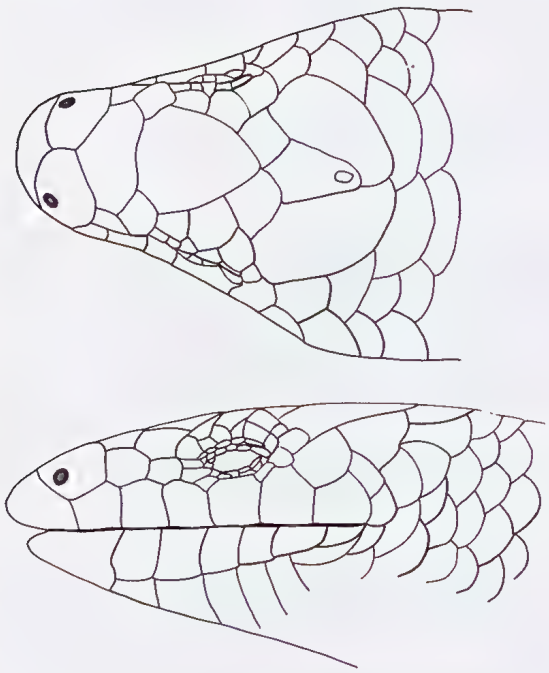

FIG. 1. *Lerista colliveri* (holotype J16181). Above: dorsal view of head. Below: lateral view of head.

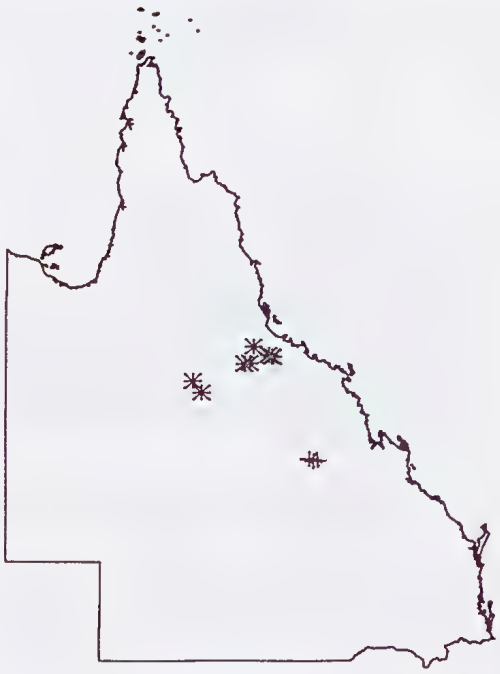

FIG. 2. Distribution of *Lerista colliveri* (*) and *L. allanae* (+).

FIG. 3. *Lerista colliveri* Red Falls, NEQ (Glenn Shea).

raven Stn, c.80km NW Hughenden at Stewart Ck (20°30'S, 143°55'E), CQ, A. Rozefelds and J. Covacevich, 7 Aug 1985; J16182-3 Hughenden (20°51'S, 144°12'E), CQ, J. Devecchi.

DIAGNOSIS

A large (maximum snout-vent length 84) *Lerista* with a movable eyelid; foreleg reduced and represented by a nubbin; and hindleg with one clawed digit. Most similar to *L. allanae* but distinguished by colour-pattern (continuous, dark, longitudinal lines dorsally and laterally; ventral scales with or without dark flecks vs longitudinal lines of dark spots dorsally and laterally; all ventral scales dark edged).

DESCRIPTION

Snout-vent length (mm): 41-84 (N 12, mean 67.4). Length of appendages etc. (% snout-vent length): hindleg 7-9 (N 12, mean 7.6), tail 111-127 (N 4, mean 118.5), head length 9-13 (N 12, mean 10.0), head width 6-8 (N 12, mean 6.7).

Nasals broadly in contact. Prefrontals widely separated. Frontoparietals narrowly (N 7) to moderately (4) separated but sometimes touching (1). Usually 2 nuchals contacting the parietals, rarely 3 (N 12, mean 2.1). Supraoculars 3, first two in contact with the frontal. Supraciliaries 5 (N 28). Loreals 2, second smaller. Presuboculars 2, second the smaller. Supralabials 6, fourth below eye. Infralabials 6. Midbody scale rows 18 (N 28). Paravertebral scales 81-94 (N 13, mean 87.7). Foreleg almost absent, represented by a nubbin in a dimple. Hindleg with one clawed digit. Lamellae under longest toe 5-7 (N 12, mean 5.9).

Dorsal and lateral ground colour tan with a pattern of more or less continuous, dark, longitudinal lines; the lines are formed by individual scales having a dark central streak; on lower flanks the lines are broken into dark-edged scales. Ventral ground colour cream; chest and belly immaculate to well-marked with dark flecks; underside of tail boldly to obscurely patterned with longitudinal lines of dark flecks. Head shields dark-edged and mottled; lips barred; loreals and temporals marked by a dark streak breaking up posteriorly.

DISTRIBUTION

From just east of Townsville, NEQ, southwest to the Hughenden area, CQ.

ETYMOLOGY

Named for Mr Stanley Colliver OBE (1908-1991) for his generosity and outstanding contributions to the Queensland Museum.

REMARKS

L. colliveri was included in *L. allanae* by Cogger (1983, 1985), Wilson & Knowles (1988) and Covacevich & Couper (1991a). The two species are similar. However, *L. colliveri* has distinct forelegs represented by nubbins while *L. allanae* has no protruding forelegs; they also differ in colour-pattern. The two species are separated by about 400km.

According to the criteria of status in Ingram & Raven (1991: 337), *L. colliveri* should be listed as '3K'.

Lerista allanae (Longman)
(Figs 3-5)

Rhodona allanae Longman, 1937:167. Holotype J6180 from Retro Station, Capella, CQ.

MATERIAL EXAMINED

J12232 Clermont (22°50'S, 147°38'E), CQ, C. Vallis, Jan 1960; J6040, 6179-80, 6238, 6308, 6429-30 Retro

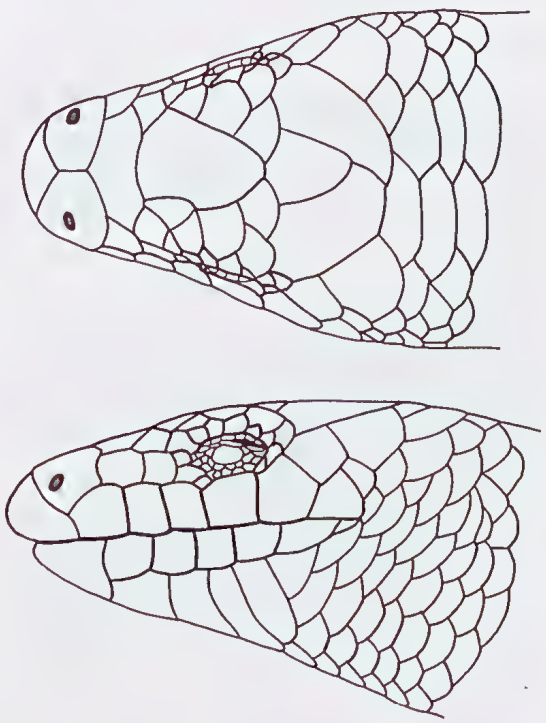

FIG. 4. *Lerista allanae* (holotype J6180). Above: dorsal view of head. Below: lateral view of head.

FIG. 5. *Lerista allanae* (holotype J6180) from Retro Station, Capella, CQ (Garry Cranitch).

Stn, Capella, via Clermont (22°52S', 147°54'E), CQ, P.C. Allan; R13819 20 miles W of Capella (23°06'S, 147°43'E), CQ, J.R. Slevin, Aug 1929.

DIAGNOSIS

A large (maximum snout-vent length 88) *Lerista* with a movable eyelid; foreleg absent (usually represented by a shallow depression); and hindleg with one, clawed digit. See diagnosis of *L. colliveri* for further differences from that species.

DESCRIPTION

Snout-vent length (mm): 61-88 (N 7, mean 76.3). Length of appendages etc. (% snout-vent length): hindleg 6-10 (N 7, mean 7.7), tail 100-104 (N 2, mean 102), head length 9-10 (N 7, mean 9.0), head width 6-8 (N 7, mean 6.4).

Nasals broadly in contact. Prefrontals widely separated. Frontoparietals narrowly (N 4) to moderately (2) separated but rarely touching (1). 2-4 nuchals contacting the parietals (N 7, mean 2.4). Supraoculars 3, first two in contact with the frontal. Supraciliaries 4 or 5 (N 8, mean 4.5). Loreals 2, second smaller. Presuboculars 2, second the smaller. Supralabials 6, fourth below eye. Infralabials 6. Midbody scale rows 18, rarely 20 (N 8, mean 18.3). Paravertebral scales 78-89 (N 7, mean 85.1). Foreleg absent, represented usually by a shallow depression. Hindleg with one, clawed digit. Lamellae under longest toe 8-9 (N 8, mean 8.6).

Dorsal and lateral ground colour tan to gray-brown; back and flanks marked by longitudinal lines of dark spots. Ventral ground colour pale with chest and belly strongly marked by dark edged scales; dark edging particularly prominent under tail. Head shields dark-edged, obscure mottled; lips barred; loreals and temporals marked by dark streak breaking up posteriorly.

DISTRIBUTION

Between Clermont and Capella, CQ, within the area 22°50-23°06'S and 147°38-147°54'E.

REMARKS

Longman (1937) described *Rhodona allanae* from three specimens. He designated J6180 as holotype but left unwritten the registration numbers of the two paratypes. Covacevich (1971) said the paratypes were J6040 and J6238 and that J6308 was a questionable alternative to J6238. However, while there is no doubt about J6040, both the dates of registration of J6238 and J6308 (28 June 1937 and 30 November, 1937 respectively) are after the date of publication of Longman's paper (24 June 1937) and thus unlikely to have been examined for the paper. Actually, the second paratype must be J6179, which was registered with the holotype and is noted as 'paratype' in the register.

According to the criteria of status in Ingram & Raven (1991: 337), *L. allanae* should be listed as '2E'. McDonald et al. (1991) rated it as '3R'. However, they included specimens of *L. colliveri* in their concept of *L. allanae*. With *L. colliveri* removed, the species is only known from over a restricted range of about 60km and has been collected only in the years 1929 by J.R. Slevin (see Slevin, 1955), 1936-1938 by Mrs P.C. Allan (inferred from the same dates of registration in the Queensland Museum register) and 1960 by C. Vallis. In the last 25 years, despite intensive searching between Clermont and Capella by many collectors, *L. allanae* has not been found again.

L. allanae is apparently sympatric with two other *Lerista*: *L. punctatovittata* (J46739-41) has been taken from c.8-10km E of Capella at Gregory Mine turnoff (23°05'S, 148°06'E) and *L. fragilis* has been collected nearby (J6181-3, 6231 Retro Stn, Capella, via Clermont; J46742-3, 46746 c.8-10km E of Capella at Gregory Mine turnoff).

ACKNOWLEDGEMENTS

We thank Steve Wilson, Gregory Czechura and David Nebauer (Queensland Museum) and Allen Greer (Australian Museum) for their advice and help; Ross Sadlier (Australian Museum) for the loan of specimens in his care; and Glenn Shea (University of Sydney) and Garry Cranitch (Queensland Museum) for their photography.

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A NESTING RECORD FOR *COERANOSCINCUS RETICULATUS* (GÜNTHER). *Memoirs of the Queensland Museum 32(1): 60. 1992:-* On 5 March, 1992, a *Coeranoscincus reticulatus* nest containing 8 eggs was found in moist soil beneath a rotten rainforest log in the Mistake Mountains, SEQ (27°58'S, 152°22'E). The log measured 107×20cm (length×width) and was in broad contact with the ground surface and situated in full sunlight (12.25pm). The eggs, just visible below the ground surface, were buried in loose soil in a 2.5cm deep depression. The substrate consisted of a soft, loamy, basaltic soil with a pH of 6.37. Surface air temperature was 27.6°C and the soil temperature within the nest was a cooler 20.0°C.

The eggs varied in length from 23.71-28.94mm (mean 27.22mm) and width from 14.0-18.55mm (mean 16.59mm). The size of the eggs seemed surprisingly large for a species with a maximum snout-vent length (SVL) of 195mm. Only one egg was accurately weighed. It measured 26.05×16.88mm and weighed 3.85gm. Six of the eggs were regular, oval shaped; one was slightly irregular oval; and one was distinctly bean shaped. Seven of the eggs appeared to be predominantly cream with black crossbands; the back and tail had an obscure, chequered effect of cream, black and brown; the pale venter scales were strongly marked with black edges producing a series of dark longitudinal lines running along the flanks, belly and under-surface of the tail.

Greer & Cogger (1985) examined shell thickness of oviducal eggs in *C. reticulatus* and suggested the species was oviparous. Our record confirms their hypothesis and the *C. reticulatus* eggs from Mistake Mountains represent the first nesting record for the species.

However, it is not possible to determine whether or not the 8 eggs found were a single clutch. From preserved museum specimens of *C. reticulatus*, McDonald (1977) recorded 3-6 oviducal eggs(N=4) in the months October-December. Thus, 8 eggs might be a single clutch but it is also possible that the nesting site was shared by more than one female. Communal nesting is well known in scincid lizards and is summarised by Greer (1989).

The fieldwork on which this paper was based is part of a study on the rainforests of SE Queensland funded by the National Rainforest Conservation Programme.

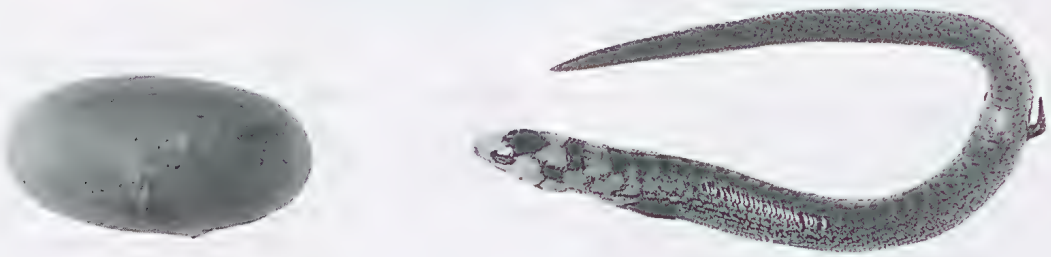

FIG. 1. *Coeranoscincus reticulatus* egg (QM J54649) and hatchling (QM J54647).

healthy; the eighth egg had a small patch of fungus on the shell.

Four eggs were carefully removed from the nest and returned to the laboratory for incubation in vermiculite. Two of these developed fungus and were preserved in 10% formalin (registered as Queensland Museum (QM) J54649 (Fig. 1) and 54650). When opened QM J54650 contained a well-developed, cream coloured embryo (SVL 39.2mm, total length 71.52mm) with conspicuous dark crossbands on the anterior half of the body.

The two eggs left incubating hatched on 2 April, 1992 (QM J54647) and 5 April, 1992 (QM J54648). Hatchling QM J54647 (Fig. 1) (SVL 59.86mm, total length 113.34mm) emerged from an egg measuring 28.07×18.55mm. Hatchling QM J54648 (SVL 58.24mm, total length 111.98mm) emerged from an egg measuring 26.05×16.88mm. Both hatchlings were similarly patterned: the head and neck regions were

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JALIJBANG 2 AND THE DISTRIBUTION OF PECKED FACES IN AUSTRALIA

BRUNO DAVID, DAVID CHANT AND JOSEPHINE FLOOD

David, B., Chant, D. & Flood, J. 1992 06 29: Jalijbang 2 and the distribution of pecked faces in Australia. *Memoirs of the Queensland Museum* **32**(1): 61-77. Brisbane. ISSN 0079-8835.

Archaeological excavations at the Jalijbang 2 rockshelter, near Katherine, Northern Territory, show that in this area pecked faces and Panaramitee type peckings are unlikely to pre-date the mid-Holocene. These results, however, are unlikely to shed light on the antiquity of pecked faces elsewhere in arid and semi-arid Australia, for the Cleland Hills, Durba Hills, Dampier, Sturt Creek, and Jalijbang pecked faces appear to be regionally distinctive. It does, however, show that the so-called *Panaramitee* artistic style consists of a broad, highly generalised set of conventions which cannot be purely understood as of having great antiquity.□ *rock art, Wardaman, Northern Territory, Australian prehistory.*

Bruno David, Department of Anthropology and Sociology, University of Queensland, Queensland 4072, Australia; David Chant, Department of Social Science, University of Queensland, Queensland 4072, Australia; Josephine Flood, Australian Heritage Commission, PO Box 1567, Canberra, Australian Capital Territory 2601, Australia; 9 November, 1991.

In a secluded sandstone gorge, 150km south-west of Katherine, N.T. (Fig. 1), are found a series of highly unusual engraved figures. When they were first observed by archaeologists during the mid 1980s, the figures were described as a minor but striking component of a broader regional body of rock art dominated by non-figurative and track peckings and figurative paintings (Lewis & McCausland, 1987). The figures themselves consist of four large anthropomorphs pecked into a near-vertical sandstone wall, three of which have their faces depicted (Figs 2-4). A further three pecked faces are located on nearby boulders (Figs 5 & 6). The site in which these occur is known as Jalijbang (spelled 'Jalikpany' by Lewis & McCausland, 1987) by the local Wardaman Aboriginal people. The pecked faces on the wall and boulders are all depicted in frontal view, and are reminiscent of the pecked faces from Cleland Hills (1000km to the south), which are commonly believed to be of great antiquity (Edwards, 1968). Lewis & McCausland (1987: 78), entertaining the idea of prehistoric inter-regional contacts between people from the Jalijbang region, Cleland Hills, and from other regions containing similar engravings, concluded that:

> 'whether or not there is any relationship between the Jalikpany figures and the complex anthropomorphic figures and/or face engravings elsewhere cannot, at this time, be determined.'

This paper is an attempt to address this issue and to investigate the antiquity of the Jalijbang figures. Furthermore, if the Jalijbang engravings can be shown to be closely related stylistically to the Cleland Hills engravings, then the antiquity of the former may shed light on the antiquity of the latter.

INVESTIGATING THE ANTIQUITY OF THE JALIJBANG PECKINGS

Jalijbang 2 is a small rockshelter with a high ceiling near the downstream end of a small gorge. The site itself has a curious setting in that it is bounded to the east by a vertical sandstone rock face, to the south by massive sandstone boulders (evidence of past roof-falls), and to the west and north by a seasonal creek. The creek bed itself consists of high quality ochre pebbles and quartzite and sandstone blocks. A small pocket of soft sediments has been preserved in the area bounded by the creek, the rock wall and the boulders, and this was made possible only because the boulders themselves protected it from the creek's northward waterflow during the wet season. Water rushes past the soft deposits at Jalijbang 2 during the wet season, detouring around the massive boulders, and flooding the pocket of soft sediments with quiet waters which deposit new silts during times of flood. It is in this protected pocket that archaeological sediments are found, preserved by the periodic addition of silts (Fig. 7) .

The large boulders near the soft sediment contain numerous engravings. Most of these consist of abraded grooves and pecked bird tracks. But

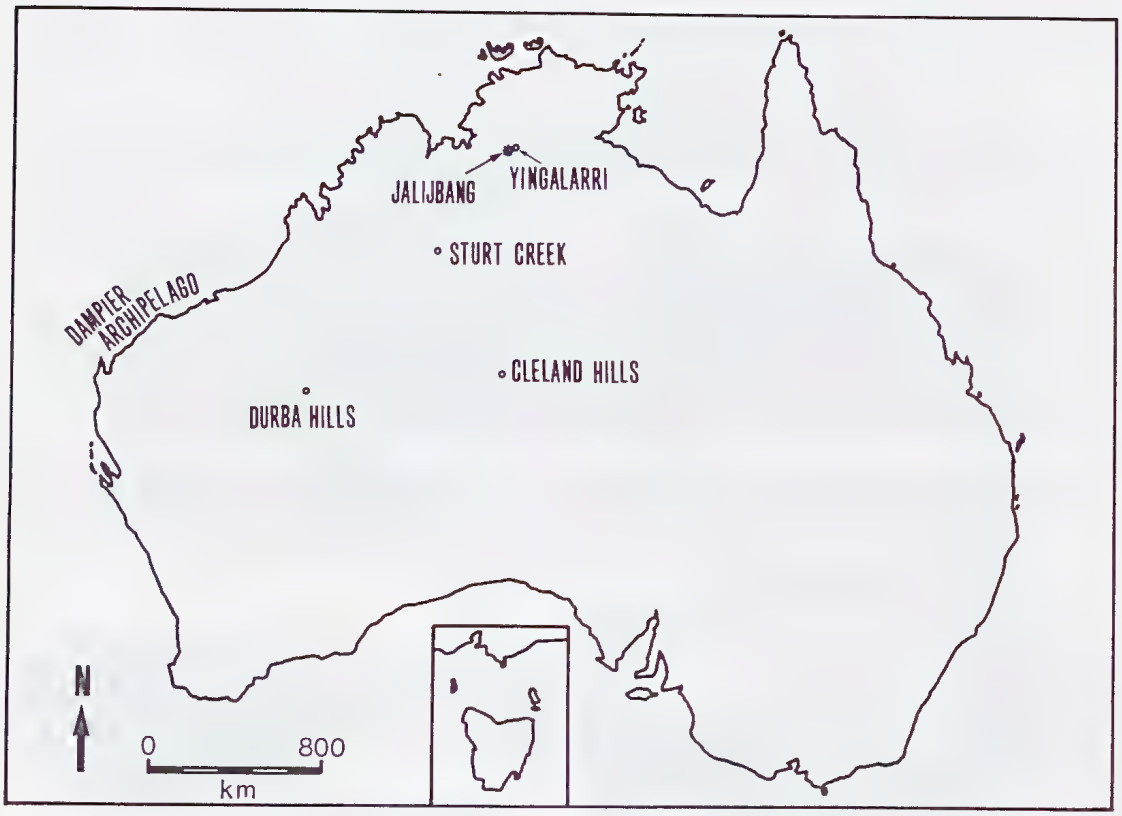


FIG. 1. Australia showing locations mentioned in text.

near the soft deposits, where the boulders meet the creek bed, lies a medium-sized boulder with a pecked face (Fig. 5). Two other pecked faces, as well as peckings of dingo-forms, occur on boulders in a rockshelter 20m upstream (Fig. 6). These boulders appear to be part of the massive sandstone boulder scree which begins at the upstream rockshelter, and end at the downstream end of Jalijbang 2. They are likely to have been deposited as a result of either instantaneous or prolonged roof-fall events.

The peckings on these boulders all occur on the boulder's upper or side surfaces (Fig. 8). None have been found on underlying boulders. Consequently, all of the boulder engravings are likely to post-date the roof-fall. Further, if the roof-fall itself was a prolonged event, then the engravings themselves were likely to have been undertaken after the *latest* episode of roof-fall, given that engravings only occur on the uppermost boulders. In excavating at Jalijbang 2, we therefore aimed at dating the roof- fall in order to obtain a maximum antiquity for the boulder engravings, which include three pecked faces (two of which occur in the upper rockshelter) reminiscent of the Cleland Hills pecked faces.

In July and August 1989, one of us (B.D.) undertook a small excavation at Jalijbang 2, immediately beneath the four pecked anthropomorphs which adorn the sandstone wall (Fig. 7). Sixteen juxtaposed 50cm × 50cm squares were excavated until compact sediments were reached, after which excavation of only four squares continued[1]. All materials were excavated in bucket spits following the natural stratigraphy (Johnson, 1979). Stone artefacts and other cultural materials greater than 2cm maximum dimension were recorded in three dimensions and bagged separately, as were all hearth stones.

Although the Jalijbang 2 sediments were well stratified, most of the individual stratigraphic laminations resulting from the alluvial deposition of silt could not be identified in situ, as variations in texture and colour were minimal.

[1]The surface sediments from the other 12 squares were excavated so that loose surface sediments would not fall into the main pit and contaminate older materials.

FIG. 2. Pecked anthropomorph located on a wall at Jalijbang 2.

FIG. 3. Pecked anthropomorph located on a wall at Jalijbang 2.

Five stratigraphic units were revealed from the excavation (Fig. 9):

Stratum 1: loose surface sediments. Fine tan-brown silts, extremely loose, containing small amounts of organic materials. Sediments are uniformly very fine.

Stratum 2: immediately underlies Stratum (SU) 1. SU 2 consists of a number of ashy and/or charcoal-rich lenses within a broader silt layer. These lenses are given separate identification (SU 2b, 2c and 2f), and most are spatially discontinuous across the excavation. SU 2 proper is a fine, silty sediment, finely laminated in some places, but the lamination was too indistinct to record except for sub-stratum 2a. The silts contain very small amounts of organic matter (including charcoal). Sediments are light tan-brown in colour. The separate sub-strata are:
SU 2a, being a 2mm thick lens of slightly darker silt;
SU 2b, a fairly well defined layer of grey ashy silt (poor in charcoal);
SU 2c, an extremely well defined charcoal concentration, containing burnt stones. It is very well defined in square E6 especially. In this layer were found the first evidence of pebbles (all burnt), many of which are fire cracked. SU 2c is black in colour, and is almost pure charcoal;
SU 2d, a fine gravel lens, with silty matrix around it. It is present in square E6, but it is ill-defined elsewhere;
SU 2e, a greyish orange silt;
SU 2f, an extremely well defined charcoal lens. It is very ashy and black in colour.

Stratum 3: extremely compact gravel and pebble layer, orange-brown in colour. Pebbles range in size from small (<1cm) to approximately 25cm maximum size. The pebbles and gravel making up SU 3 appear similar to the materials which currently make up the adjacent creek bed. The boundary between SU 2 and SU 3 is well defined.

Stratum 4: decomposing sandstone, mottled reddish yellow. Intersection with overlying SU 3 is ill-defined, spanning approximately 3cm.

Stratum 5: solid sandstone. This is the basal stratigraphic unit consisting of large boulders with relatively flat surfaces. Excavation could not proceed into or below Stratum 5 because of the size of the boulders.

Radiocarbon Dates

Two radiocarbon dates were obtained:

FIG. 4. Pecked anthropomorph located on a wall at Jalijbang 2.

a. 260± 60BP (New Age; Conventional Age is 250±60BP) (Wk-1551). This date is from a good charcoal sample from Square E6, XU 6, and dates the uppermost hearth excavated (SU 2c) (^{13}C permil = -26.6). This hearth is a well-defined charcoal and hearth stone lens which is assumed to have been created as an archaeologically instantaneous event.

b. 1040±60BP (New Age; Conventional Age is 1010±60BP) (Wk-1550). This dates the lowermost hearth (SU 2f), and comes from a good quality charcoal sample from Square F6, XU 10 (^{13}C permil = -26.0).

Occupation at Jalijbang 2

Human occupation at Jalijbang 2 began sometime before 1040±60BP. Low density deposition rates of stone artefacts are found throughout the deposits, although peak rates occur in association with the two hearths (around 260BP and 1040BP) (Table 1). Only two small fragments of bone were found (both in post-260BP times), whilst hearth stones and heat-shattered burnt rocks are associated with the uppermost hearth. Ochre occurs, but it is difficult to associate its presence with artistic activities, as the creek bed itself contains vast numbers of ochre pebbles, and periodic floods can be expected to deposit very small fragments of ochre with the deposited silts. Ochre pebbles were also used as hearth stones during use of the uppermost hearth. No in situ ochre fragments exhibit any signs of use wear (Appendix 1).

Although stone artefacts occur below the bottom hearth (1040±60BP), their numbers are very low. These low rates are associated with SU 3 and 4, the gravel and sandstone layers below the alluvial silts and hearths. The gravels themselves indicate the presence of creek flow in this section of the site sometime in the past (in pre-1040BP times), although the large boulders were present to the immediate south during that time (as indicated by the underlying SU 5 boulders in the excavations). An extension of the depth-age curve dates the uppermost surface of the in situ sandstone boulders (SU 5) to 2880BP, although the presence of a different stratigraphic unit between it and the dated silts (SU 2) means that this date is likely to be a very general indication only of the age of the roof-fall which resulted in the boulder deposit. Consequently, this extrapolated date should be used with caution, and is presented here as a very general indication only of the order of magnitude which we can expect the age of the roof-fall underlying the cultural deposits to be. It is not known if cultural materials occur below the boulders, as excavation could not proceed below them.

Other Dates

Two other independent sources indicate a mid- to late-Holocene antiquity for the end of the roof-fall expressed stratigraphically as SU 5:

1. On boulders located in a rockshelter 20m upstream from Jalijbang 2 (at Mennye-ya), a large, exfoliated boulder contains pecked dingoforms on its upper surface. These boulders were likely to have been deposited during the same roof-fall event(s) which resulted in the creation of the scree-slope at Jalijbang 2, and dated to approximately pre-2880BP by reference to the depth- age curve. As dingoes first arrived in Australia around 3500 years ago (Solomon & David, 1991), the peckings must have been undertaken sometime after that time. This does not mean that the boulders were necessarily deposited after this time, but does indicate that at least some of the art on them were done in mid-

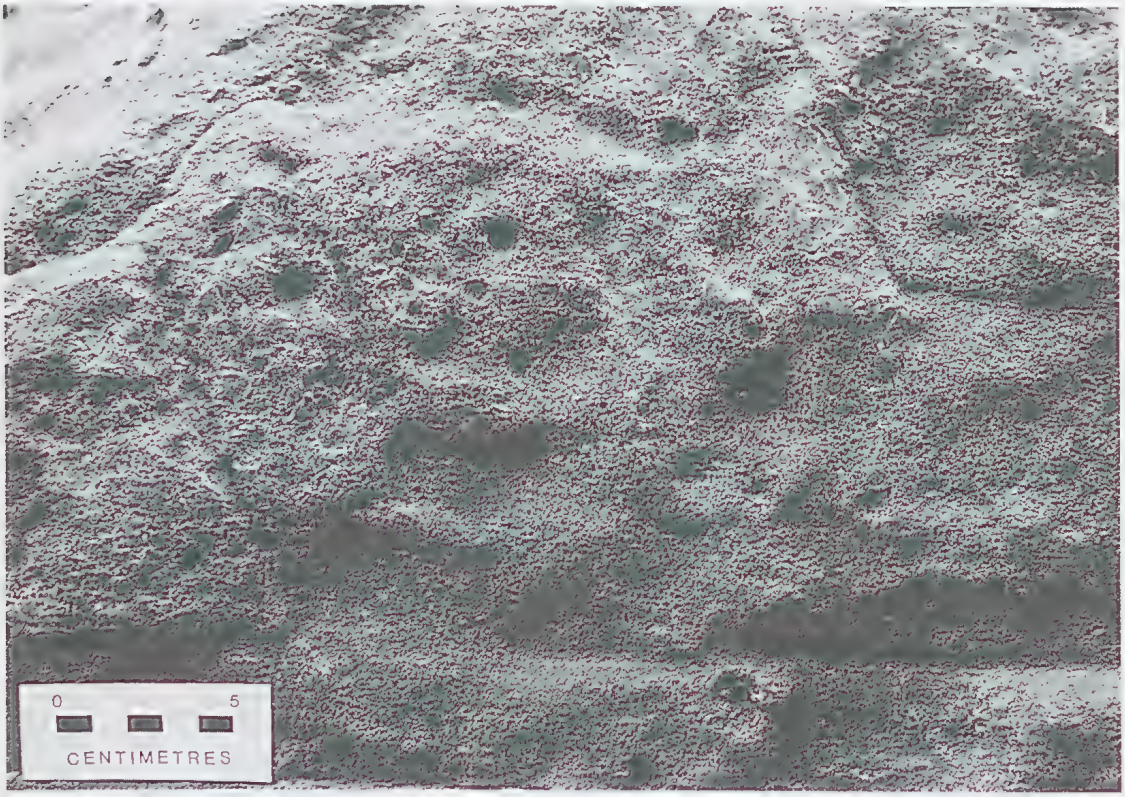


FIG. 5. Weathered pecked face from creek-bed boulder, Jalijbang 2 (see Fig. 7 for location of boulder).

TABLE 1. Deposition of materials, Squares E6 and F6. All rates are per m^2 per 100 years.

SQUARE	XU	1	2	3	4	5	6	7	8
E6	1-5	<0.1	15.5	3.6	0.1			0.22	1989AD–260BP
E6	6–8	195.3	15800.0	1750.0		300	24.5	411.2	260BP
E6	9–11	<0.1	31.8	3.3				0.45	260–1040BP
E6	12–22	<0.1	5.54	3.5				105.9	1040–2880BP
F6	1–3	<0.1	6.5	1.6				0.08	1989AD–260BP
F6	4	5.4	1600.0	40.0				8.8	260BP
F6	5–9	<0.1	34.4	30.1				4.0	260–1040BP
F6	10–11	185.6	1200.0	9680.0			99.6	1467.6	1040BP
F6	12–21	<0.1	1.3	1.1				10.5	1040–2880BP

1=CHARCOAL (KG). 2=LITHICS (#). 3=LITHICS (G). 4=BONE (G). 5=HEARTH STONES (#).
6=OTHER BURNT ROCK (KG). 7=RESIDUE (KG). 8=YEARS IN SPITS

to late-Holocene times. The other peckings on this and nearby boulders show a similar degree of patination (moderate to heavy) as the dingo peckings, indicating probable comtemporaneity.

2. A cortex sample was extracted from a nearby boulder by Alan Watchman (pers. comm., 1988). The cortex was examined by Watchman (1990), who found a thin, microscopic layer of organic-rich materials at its base. The organic materials were extracted and dated through AMS, where a date of 4010±300 was obtained (Watchman, 1990). As the sample came from near the base of the cortex, it dates the beginnings of cortex development, and hence when

FIG. 6. Pecked faces. A, I-N=Dampier. B-C=Jalijbang boulders. D-G=Cleland Hills. H=Durba Hills. After Dix (1977) and Lewis & McCausland (1987).

FIG. 7. Plan of Jalijbang 2. Fine-dashed area is large boulder scree.

the boulder probably became exposed to the elements. 4010±300BP is therefore likely to represent the antiquity of the boulder's deposition to its current position.

Discussion of Antiquity of Boulders at Jalijbang 2

Three independent investigations all point to a mid- to late- Holocene antiquity for the end of the roof-fall which resulted in the massive boulder scree at Jalijbang 2. The in situ sandstone boulders located in the excavation were themselves tentatively dated to around 2880BP by extension of the depth-age curve. A major problem with this dating is that it assumes a steady sedimentation rate below the lowest radiocarbon date, and hence, by itself, the resultant chronology can only be taken as a general approximation at best. When compared to the cortex date (4010±300BP) and the presence of pecked dingo-forms on boulders from the adjacent scree deposits (post-3500BP), however, the depth-age calculation appears to be of the correct order of magnitude. The roof-fall at Jalijbang 2 appears to have ended around 3000 to 4000 years ago.

Antiquity of Pecked Faces

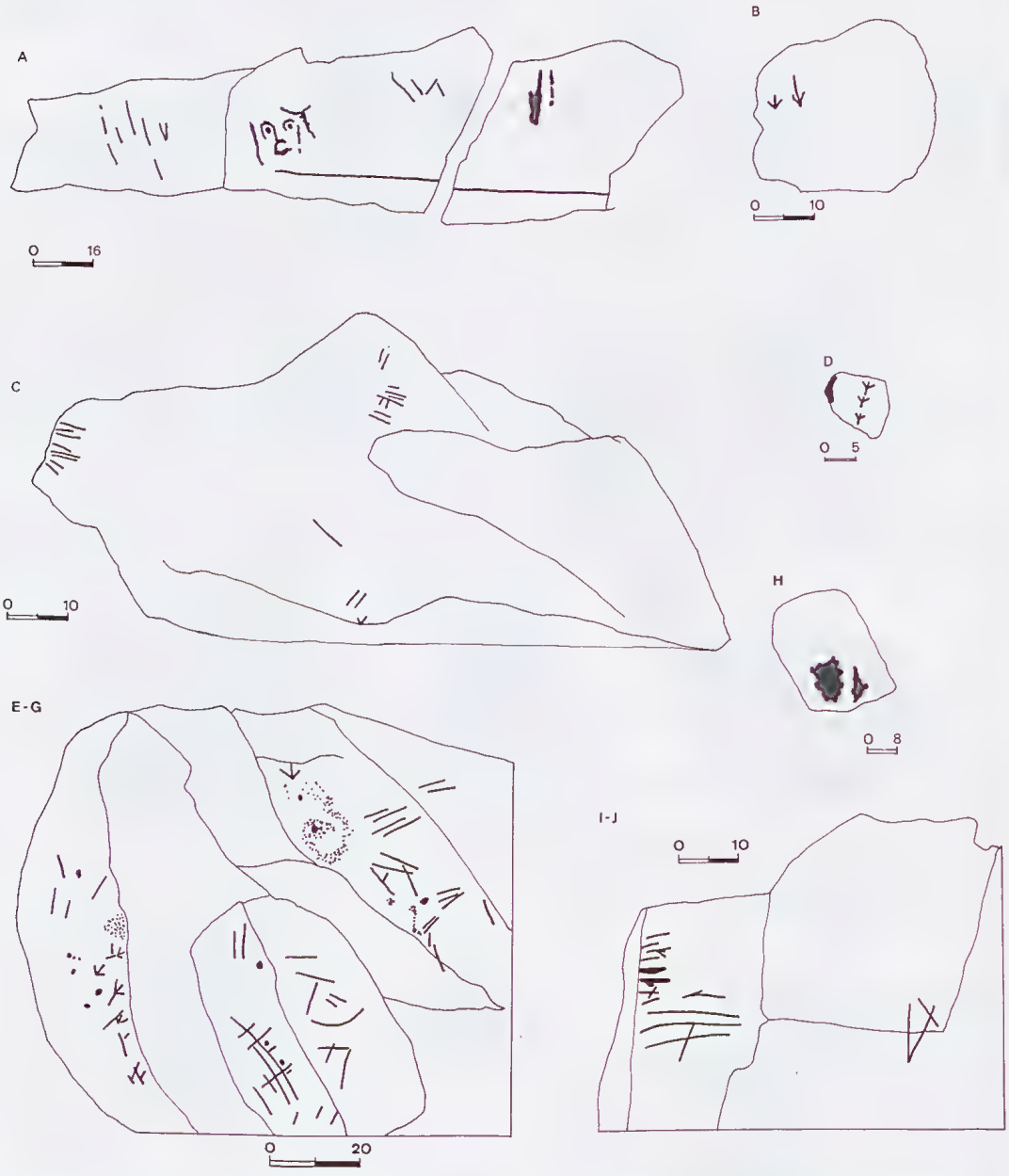
Given a likely mid- to late-Holocene antiquity for the end of the roof-fall at Jalijbang 2, it is also likely that the pecked faces and other engravings on the boulders are of a similar antiquity. The pecked face in the creek bed at the base of the boulder scree (Fig. 5) is also unlikely to pre-date the mid-Holocene as the annual waterflow in the creek can be expected to have obliterated the pecking were it to have greater antiquity. It is notable that during pre-3000BP times precipitation was significantly higher than at present, making it even more unlikely that this pecking would have survived (Chappell & Grindrod, 1983).

As all of the boulder engravings at Jalijbang 2 are located on the upper and side surfaces of the uppermost boulders only, it is also likely that all engravings post-date the *latest* episode of roof-fall (3000 to 4000BP). These engravings include pecked faces and bird tracks and abraded grooves.

The peckings on the rock wall, however, are much more difficult to date. It is possible that the roof-fall which terminated around 3000 to 4000 years ago resulted in the creation of the rock wall itself (and hence the peckings postdate this time), but it is also possible that the current rock wall existed before the roof-fall. If the former was the case, the peckings on the wall would be roughly contemporaneous with the boulder engravings. It is possible, however, that the wall engravings are older, although they possess similar patination to the adjacent boulder peckings (supporting general contemporaneity, although degree of patination can vary widely even within localised areas). In any case as will be shown below the boulder pecked faces are stylistically different from the wall ones, and therefore the antiquity of the former cannot be used to date the latter on stylistic grounds. In short, the boulder engravings probably date to the mid- to late-Holocene, whilst the antiquity of the wall engravings is unknown.

We investigate below the possiblity of determining the antiquity of other pecked faces from arid and semi-arid Australia by investigating stylistic distributions of pecked faces. We specifically ask the question, are the dated (boulder) pecked faces at Jalijbang 2 of a purely

FIG. 8. All of the abraded and pecked figures located on the boulders at Jalijbang 2. All scales are in centimetres. Continued on next page



local style, or are such faces found elsewhere also; if the latter, can the antiquity of the Jalijbang 2 faces reveal information on the antiquity of pecked faces elsewhere?

To address these questions, we undertake preliminary analysis of all published pecked faces from Australia which have a basic resemblance to those of Jalijbang.

THE REGIONAL OCCURRENCE OF PECKED FACES

Wardaman Country (Jalijbang and Yingalarri)

The pecked faces from Jalijbang can be divided into two groups, those on boulders and those on the wall. The three faces found on the

FIG. 8. Continued from previous page. All of the abraded and pecked figures located on the boulders at Jalijbang 2. All scales are in centimetres.

rock wall are very similar to each other: they all have concentric circles for the eyes, ears, noses, and broadly cylindrical outlined faces. They also have full or partial bodies. The faces pecked on boulders, however, exhibit neither bodies nor ears, and consist only of non-concentric eyes. Only one of the boulder pecked faces has a nose. The boulder faces are generally smaller than those located on the wall, and were created by a small number of separate, pecked lines (6, 7 and 7 for the boulder faces, compared to the 14, 20 and 26 lines that make up the pecked faces on the wall[2]). In short, the Jalijbang pecked faces can be divided into two distinct stylistic groups, the structurally complex wall faces, and the more generalised boulder ones.

A pecked face was also recently rediscovered by the authors at Yingalarri, 20km east of Jalijbang (and still within Wardaman country). This pecking (see Flood et al., in press), like the Jalijbang boulder ones, lacks the structural complexity of the Jalijbang wall peckings (see Table 2 for traits present).

Cleland Hills

Edwards (1968) reported on the occurrance of fifteen pecked faces from the Cleland Hills, 1000km south of Jalijbang. Of these, five figures are illustrated in his and subsequent reports (Edwards, 1968; Dix, 1977) (many of the others are badly weathered and difficult to distinguish). The Cleland Hills faces have been linked stylis-

[2] These numbers refer to the separate lines that make up the *faces* of each figure only.

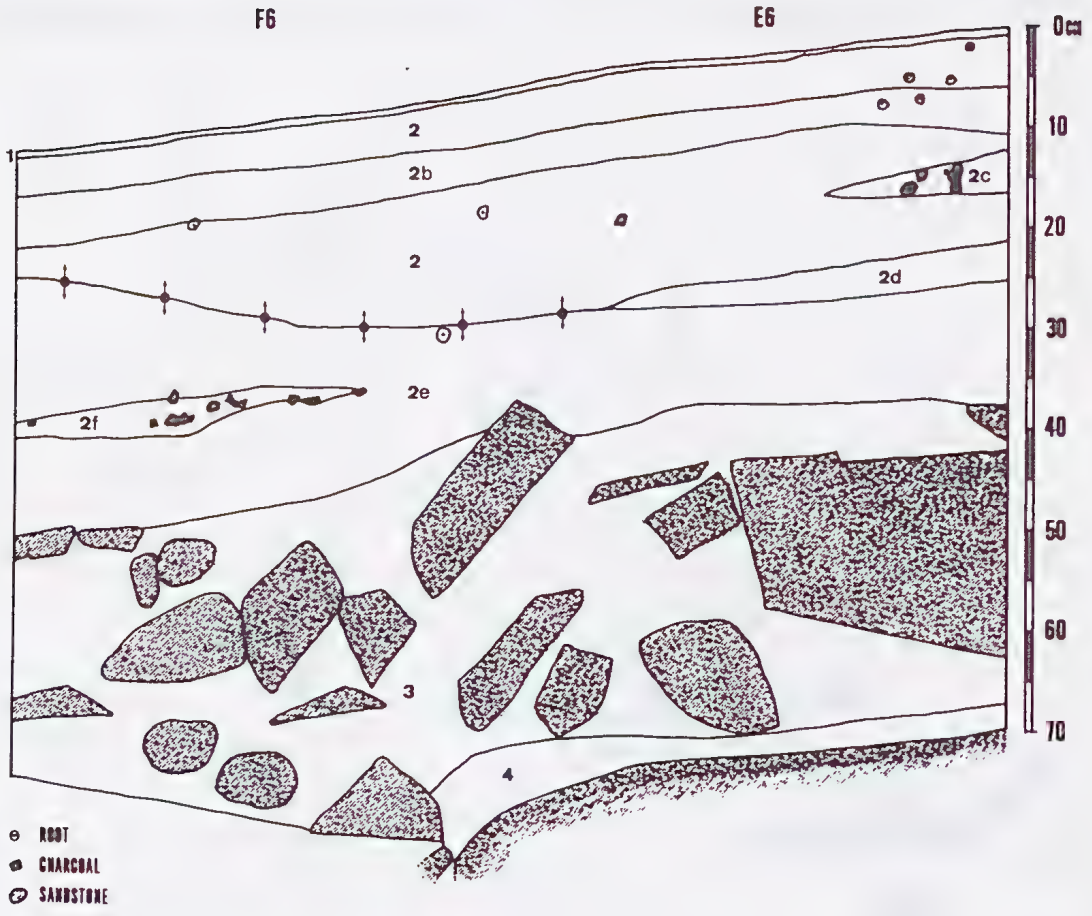


FIG. 9. Section drawing, Jalijbang 2.

tically to those from Jalijbang, Dampier, Sturt Creek and elsewhere (e.g. Dix, 1972, 1977; Lewis & McCausland, 1987), and have been considered to have considerable antiquity by virtue of their advanced state of patination. Yet the Cleland Hills faces contain a suite of characteristics not found in pecked faces elsewhere. These faces are generally pear- shaped or heart-shaped with noses depicted whilst their mouths are shown as straight or curved lines (at Jalijbang mouths on the wall faces are represented as single dots). Eyes consist of concentric circles, but unlike the Jalijbang wall faces, they were executed by a small number of separate pecked lines only (7, 8, 9, 10 and 10 for the five faces illustrated in Edwards, 1968 & Dix, 1977). We will return to these points below.

Dampier

The pecked faces from the Dampier region of Western Australia are relatively varied in style. One of their dominant features is the representation of hair on many figures, although this is not always so. Other characteristics are concentric circle eyes, and the enclosure of the head in an outline. The nose is sometimes represented, but ears are not and heads are never pear-shaped. The Dampier faces include figures created by numerous separate lines (up to 32) as well as some created by a few lines only (as few as seven). The former are more common.

Durba Hills

The Durba Hills (W.A.) face reported by Dix (1977) exhibits hair and concentric circle eyes, but nose, ears, body, and head enclosure are missing. It is reminiscent of the Dampier faces, and this is especially so of the hair and of the parallel lines below the eyes.

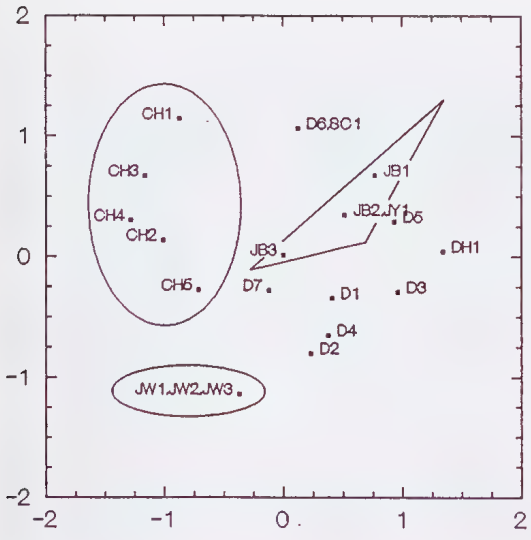


FIG. 10. MDS map based on eight qualitative variables.

Sturt Creek

The Sturt Creek pecking has, like the Cleland Hills faces, a linear mouth. The head is enclosed and attached to a full body (Crawford, 1968; Walsh, 1989). It is in this way reminiscent of the Jalijbang 2 wall peckings, although unlike the latter, it does not have concentric circle eyes, ears or nose.

Regional Variability

The Jalijbang 2 boulder and wall pecked faces are stylistically different from each other, especially with respect to the presence or absence of concentric circle eyes, nose, ears, and associated bodies. Similarly, whilst the wall faces are composed of many separate pecked lines, the boulder faces contain considerably fewer lines (Table 3). The pecked face located on an exposed boulder at Yingalarri is stylistically similar to the boulder faces from Jalijbang 2.

To the south and southwest of Jalijbang, however, are found a number of pecked faces which, although superficially resembling the Jalijbang faces, are regional variations of the same theme (pecked faces). Such peckings are characteristic, although minor, components of some arid and semi-arid zone pecked assemblages. Since they are not found in more humid zones, their shared presence in arid Australia has often entertained the possibility of inter-regional interactions linking the places where they are found in a vast desert social network. But before this idea can be properly entertained, the presence of shared stylistic traits should be demonstrated. The presence of pecked faces in different areas, by itself, cannot be taken to signify a single artistic convention - pecked faces are not necessarily structurally complex endeavours, and only a limited number of traits (e.g. presence of eyes and head outline) are needed to make a picture resemble a face. In other words, the presence of non-essential lines (e.g. ears are not needed to make a face-form), and/or of particular combinations of features, are needed to be shared before two geographically separate bodies of pecked faces can be deemed to be represented by a single stylistic convention.

In examining the similarities and differences between the known pecked faces of Jalijbang, Yingalarri, Cleland Hills, Durba Hills, Dampier and Sturt Creek, we began by identifying whether certain traits were present or not. These traits are:

1. hair or head-dress;
2. nose;
3. ears;
4. linear mouth (as opposed to a dot or an enclosed area);
5. concentric circle eyes (a circle around a dot is not considered a concentric circle);
6. pear or heart shaped head;
7. head enclosed by an outline;
8. associated body.

The traits themselves were chosen to highlight stylistic variation. It was noticed that some traits were present in all pecked faces (e.g. eyes), whilst others were present in some only. The traits chosen specifically represent the major traits present in a number of peckings but not all of them. A Multi- Dimensional Scaling (MDS) statistic was subsequently undertaken to reveal how the separate faces cluster stylistically with each other, on the basis of the combination of the eight identified traits. Our main aim was to determine whether or not the faces from each region clustered together and, if so, did these clusters separate out conspicuously from the other regions.

The variables used in the MDS were the eight traits enumerated in Table 2. MDS is a set of mathematical techniques which enables the mapping of units (pecked faces) as points in geometrical space, reducing the number of dimensions (eight in our case) to two. It enables the user to locate the units in a spatial configuration - a 'map' (Fig. 10) (Alvey et al., 1982: 122). Ulsaner (1978: 5) writes: 'Once we have located the ... points in (multi-dimensional) space, we

TABLE 2. Traits present in the pecked faces analysed.

	HAIR	NOSE	EARS	LINEAR MOUTH	CONC. EYES	PEAR-SHAPED HEAD	HEAD ENCLOSED	BODY
1. JAL WALL		X	X		X		X	X
2. JAL WALL		X	X		X		X	X
3. JAL WALL		X	X		X		X	X
4. JAL BOULDER								
5. JAL BOULDER							X	
6. JAL BOULDER		X					X	
7. YINGALARRI							X	
8. CLELAND HILLS		X		X		X		
9. CLELAND HILLS		X		X	X	X	X	
10. CLELAND HILLS		X		X	X	X		
11.CLELAND HILLS		X		X		X	X	X
12. CLELAND HILLS		X			X	X	X	
13. DURBA HILLS	X				X			
14. DAMPIER	X	X					X	
15. DAMPIER	X	X					X	X
16. DAMPIER	X				X		X	
17. DAMPIER	X	X			X		X	
18. DAMPIER					X			
19. DAMPIER				X			X	X
20. DAMPIER		X			X		X	
21. STURT CREEK				X			X	X

seek to determine the hidden structure, or theoretical meaning of this spatial configuration'.

The importance of MDS is that it provides a way of reducing the data to two dimensions. These two dimensions represent the 'hidden structure' of the data. Identification of key differences between the pecked faces was determined by identifying those that stand out or cluster together on the MDS map. To do this, statistical proximity values between units (pecked faces) are computed. 'The larger the dissimilarity (or the smaller the similarity) between two objects, as shown by their proximity values, the further apart they should be in the spatial map' (Kruskal & Wish, 1978: 7).

The results of the MDS shows a high level of regional clustering. As expected, the Jalijbang 2 wall and boulder peckings separate out. The Yingalarri figure, also located within Wardaman country, cluster with the Jalijbang 2 boulder faces. The Cleland Hills faces separate out well, as do the Dampier and Durba Hills faces. The Sturt Creek figure is similar to one of the Dampier figures, but all other pecked faces-are regionally discrete (Fig. 10). In short, the arid and semi-arid zone pecked faces consist of a series of regionally specific figures, differentiated by the presence or absence of particular traits. It is the combination of such traits which gives each region its stylistic particularity. Unfortunately, the published information and illustrations of these pecked figures do not reveal enough information to determine whether or not there are also regionally specific metrical differences. We have nevertheless briefly attempted to gather information on this question by quantifying the following:

a. the ratio of the distance between the eyes (taken from centre of eyes) to width of face at that plane;

b. the maximum width to height ratio (the former being at a parrallel to the eye plane, and the latter perpendicular to width);

c. the number of separate pecked lines making

TABLE 3. Quantitative data.

	DBE:FW	W:H	# OF LINES
1. JAL WALL	0.36	0.79	26
2. JAL WALL	0.39	0.77	14
3. JAL WALL	0.57	0.93	20
4. JAL BOULDER	0.53	0.84	7
5. JAL BOULDER	0.54	1.20	6
6. JAL BOULDER	0.41	0.87	7
7. YINGALARRI	0.36	0.57	8
8. CLELAND HILLS	0.64	0.93	7
9. CLELAND HILLS	0.50	1.00	10
10. CLELAND HILLS	0.55	1.00	10
11. CLELAND HILLS	0.56	0.90	9
12. CLELAND HILLS	0.45	1.20	8
13. DURBA HILLS	0.37	0.71	31
14. DAMPIER	0.45	0.63	25
15. DAMPIER	0.50	1.08	16
16. DAMPIER	0.32	1.22	32
17. DAMPIER	0.52	0.78	28
18. DAMPIER	0.59	1.42	7
19. DAMPIER	0.30	0.45	8
20. DAMPIER	0.39	1.14	13
21. STURT CREEK	0.47	0.79	11

DBE=DISTANCE BETWEEN EYES. FW= FACIAL WIDTH . W=WIDTH. H=HEIGHT

up the faces (if a body is present, it is not included in the quantification).

The MDS undertaken on this data set does not reveal the distinct regional character revealed by the previous analysis (Table 3, Fig. 11). Nevertheless, the Cleland Hills faces separate out well from the other peckings, accentuating their regional specificity. Detailed quantitative analysis will have to await the availability of further quantitative data from each of the pecked figures.

DISCUSSION

The rock art located in Wardaman country, Northern Territory, is widespread and stylistically diverse. A very small component of the Wardaman rock art assemblage consists of pecked faces, some of which also have associated torsos. Within Wardaman country, the Jalijbang and Yingalarri pecked faces are superficially reminiscent of the Cleland Hills faces. These have often been infered to have considerable antiquity because of their stated advanced state of patination. Published photographs, however, show that some of these peckings are moderately patinated only (e.g. Edwards, 1968). In any case patination, especially of peckings in open sites, is not necessarily an indication of great age, as is testified by the existence of patinated post-contact graffiti. Similarly, the Jalijbang pecked faces have been claimed to be of considerable antiquity, but there is no strong reason to believe this is necessarily the case. On the contrary, the pecked faces found on boulders in Jalijbang 2 and in a nearby rockshelter (Mennye-ya) are likely to date to the last 3000-4000 years. Because these figures are stylistically distinct from pecked faces from other parts of arid and semi-arid Australia, however, their antiquity cannot in this way be used to infer the ages of pecked faces elsewhere.

Furthermore, the engravings found on the Jalijbang 2 boulders also include pecked bird tracks and linear designs and abraded grooves. Such peckings have often been characterised as typical components of the so-called Panaramitee engraving tradition. Such engravings are often believed to have considerable antiquity (e.g. Maynard, 1977), but at Jalijbang 2 they appear to have a maximum age of 3000-4000 years BP. Abraded grooves and pecked bird tracks, however, have also been found at the Yingalarri 1 excavations (Mulvaney, 1975), where they were dated to at least 5000BP. Abraded grooves are also known to have been created in the Jalijbang and Yingalarri areas during recent times (Flood

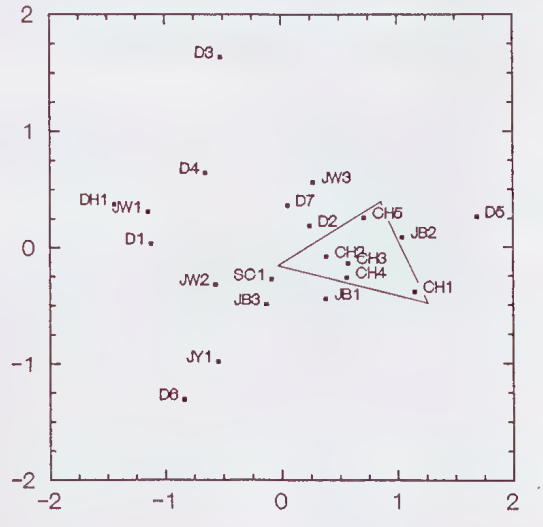


FIG. 11. MDS map based on three quantitative variables.

et al., in press). It is therefore likely that peckings and abraded grooves were part of a long artistic tradition in Wardaman country, spanning the period from pre-5000BP times to the ethnohistoric present. This pattern appears to be similar to that found by Nobbs & Dorn (1990) in the Olary region to the south, where cation-ratio dates revealed a broad range of non-figurative and track peckings spanning approximately 30 000 years of prehistory (but see Watchman, in prep.). In the Wardaman and Olary regions at least, the 'Panaramitee' (as defined stylistically by Maynard, 1977) has had a long history, broken only in recent times by the White intruders who constrained the local people access to the lands in which they engraved and painted.

In short, although some of the engravings found in Wardaman country have been dated to pre-5000BP times by Mulvaney (1975), there is no evidence that the pecked faces from Jalijbang 2 have any great age. Although their precise antiquity remains a matter for speculation, excavations at the site point towards a likely mid- to late-Holocene antiquity. We say this through circumstantial evidence only:

1. the occurrence of extensive roof-fall predating approximately 3000BP *may* indicate that the main, pecked wall at Jalijbang 2 did not exist before that time;

2. boulder peckings occur only on the upper and side surfaces of boulders believed to have been deposited in their current positions during the mid- to late-Holocene. Given the absence of peckings from the underneath surfaces, the peckings are likely to have been undertaken only after the boulders were deposited in their current positions;

3. the pecked face on the boulder in the creek bed at Jalijbang 2 has not been totally obliterated by water action, implying that it may not be of great antiquity;

4. other nearby peckings, also associated with the roof-fall boulders relating to points 1 and 2 above, contain peckings of dingoes, which because of their known antiquity in Australia must post-date approximately 3500 to 4000 years BP;

5. analysis of cortex on a boulder near Jalijbang 2 indicates that cortex development began approximately 4000 years ago. Because of its proximity to Jalijbang 2, it is likely that this boulder resulted from the same roof-fall activity as the boulders currently forming the scree-slope into the site itself (points 1 and 2 above), in support of a similar antiquity for the roof-fall itself (creation of the boulder surface where cortex development ensued).

Although the Jalijbang 2 boulder peckings (and wall peckings to a lesser extent) are more likely to be of mid- to late-Holocene age, it has not been possible to gain information on the antiquity of other, similar engravings from the Northern Territory and Western Australia. The latter are stylistically distinct from the pecked faces found in Wardaman country, with each area possessing regionally-distinctive pecked faces. These findings question the previously widely-stated belief that pecked faces from many parts of the Australian arid and semi-arid zones were similar and presenting material evidence for a broad, interactive social network which linked central Australia into a more or less unified 'desert culture'. On the contrary, this is nowhere reflected in the distribution of pecked faces which emphasise the regional specificity of artistic traditions in Australia's arid core.

ACKNOWLEDGEMENTS

We would like to thank the Wardaman people for allowing us to excavate at Jalijbang, Earthwatch for financial support and fieldwork assistance, and A.I.A.T.S.I.S. for funding the carbon dates. Bryce Barker, Ian McNiven, Philip Jones and an anonymous referee made useful comments on an earlier draft.

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APPENDIX 1
List of materials excavated from Jalijbang 2.

SQUARE E6												
XU	1	2	3	4	5	6	7	8	9	10	11	SU
1	<0.1			2.2						0.25	0.2	1
2	2.4			6.8		28				0.25	3.6	2+2B
3	17.0	5	0.3	42.2		1				0.25	3.5	2+2B
4	2.9			26.2		<1				0.25	1.4	2
5	9.1	7	2.3	4.8	0.1	10	0.1			0.25	1.9	2C
6	91.5	49	14.7	4.4		440		1		0.25	3.2	2C
7A	219.6	9	0.8	7.8		1		2	245	0.12	3.7	2C
7B	2.1			0.5						0.13	3.7	2
8	3.5	5	0.1	4.5						0.05	2.7	2C
9	12.0	11	1.0	2.9		140	0.5			0.25	3.8	2D
10	9.1	46	5.3	13.2		66	0.3			0.25	2.8	2E
11	11.7	5	0.2	36.8		377				0.25	3.6	2E
12	6.1	5	9.8	25.6		333				0.25	2.5	2E
13	1.8	5	2.9	27.0		500	0.1			0.25	2.5	2E
14	0.7	3	0.6	1.1		200	0.1			0.16	3.6	2E
15	1.2	6	1.1	37.6		3000				0.25	3.3	3
16	0.1			0.6		1800				0.24	3.0	3
17	0.1			0.4		1900				0.19	5.6	3
18				0.1		1500				0.19	4.0	3
19		1	0.2	0.1		3000				0.19	4.3	3
20	<0.1	2	0.2	1.0		3500				0.22	2.7	3
21	<0.1	1	1.1			1500				0.21	4.7	3

APPENDIX 1 cont.

SQUARE F6												
XU	1	2	3	4	5	6	7	8	9	10	11	SU
1	<0.1			2.9							0.1	1
2	7.0	4	0.8	10.5							4.6	2
3	8.0	1	0.4	23.4							2.0	2B
4	13.6	4	0.1	19.5							3.3	2+2C
5	3.7	23	2.1	4.3							2.4	2
6	3.5	9	51.0	2.5							3.1	2E
7	7.2	9	0.3	3.5							4.5	2E
8	6.1	18	2.7	6.9							4.3	2E
9	13.0	8	2.5	2.5							2.7	2E
10	453.1	2	23.1	1.0			0.2		249		3.4	2F
11	10.8	1	1.1	0.3							2.8	2E+2F
12	2.4	1	0.1	49.0							2.5	3
13	0.4	5	5.1	13.7							4.5	3
14	0.2			21.0							2.9	3
15				55.7							4.6	3
16				31.5							2.4	3
17	<0.1			20.5							4.2	3
18				7.0							4.7	3
19				8.9							4.6	3
20											2.8	3
21	<0.1			0.2							4.3	4
SQUARE E7												
1				2.9							0.1	1
2	0.7			8.5	0.3						3.0	2
3	1.5			17.2							3.6	2
4	9.5	14	8.2	5.9					38.1		3.8	2
5	37.1	9	3.8	13.7				3	48.2		2.1	2
6A	107.1	21	1.3	2.3				3	1016.9		4.9	2C
6B	6.1			10.1			0.1		14.4		4.9	2
7	4.7	1	3.0	0.8					22.7		2.6	2C
8	5.5	3	0.5	9.3							3.6	2
9	21.7	4	6.9	10.6							3.8	2
10	14.3	4	1.1	1.6					26.7		2.5	2F
11	11.8			1.4					122.4		0.9	2F
12	3.1	4	2.4	5.9							1.8	3
13	0.1	3	3.2	0.1							5.7	3
14	0.1	1	0.7	0.1							2.8	3
15				0.6							5.0	3
16		1	3.0	0.1							4.5	3+4
17				0.1							2.7	4

APPENDIX 1 cont.

SQUARE F7												
XU	1	2	3	4	5	6	7	8	9	10	11	SU
1	0.1			0.6							0.1	1
2	0.5			4.0							3.6	2+2A
3	1.0	7	0.4	16.2							3.9	2+2B
4	3.2	9	23.6	6.5			0.1				5.1	2
5	2.9	8	1.4	3.1							3.9	2E
6	4.4	3	0.1	7.0			0.1				4.0	2E
7	1.1			3.0							1.2	2E
8	52.1	9	1.1	20.6			<0.1				2.5	2E
9	2.0	1	<0.1	7.3							3.2	2E
10	366.1	10	204.1	16.0			0.2	5			3.7	2F
11	302.6	2	2.9	6.6							3.8	2F
12	9.4	1	77.3	4.7							2.6	2E
13	0.1	4	2.6	22.6							4.3	3
14	<0.1	3	1.3	1.0							4.5	3
15	<0.1			0.5							3.6	3
16		1	1.8	0.2							3.6	3+4
17	<0.1			0.1							2.2	4

PERIPHERY SQUARES									
SQUARE	XU	1	2	3	4	7	12	13	SU
D4	1	0.4			5.7		1	<0.1	1
D5	1	0.1			1.8				1
D6	1	<0.1			1.9				1
D7	1				0.4				1
E4	1	1.4	1	<0.1	7.2	0.1			1
E5	1	0.1			5.0				1
F4	1	5.5			66.2		2	<0.1	1
F5	1	0.1			1.7				1
G4	1	1.5			5.5				1
G5	1	1.1			4.8				1
G6	1	0.6	2	0.3	8.0				1

1=CHARCOAL (G). 2=LITHICS (#). 3=LITHICS (G). 4=OTHER ORGANICS (G). 5=BONE (G). 6=OCHRE (G) (NOTE DATA PRESENTED FOR E6 ONLY). 7=$CaCO_3$ ROOTS (G). 8=HEARTH STONES (#). 9=OTHER BURNT (HEAT-SHATTERED) ROCKS (G). 10=AREA EXCAVATED (M^2) (NOTE DATA PRESENTED FOR E6 ONLY). 11=MEAN THICKNESS OF XU (CM) (NOTE DATA NOT PRESENTED FOR PERIPHERY SQUARES). 12=LAND SNAILS (#). 13=LAND SNAILS (G).

REVISION OF *SARMATIUM* DANA (CRUSTACEA:BRACHYURA: SESARMINAE) WITH DESCRIPTIONS OF THREE NEW SPECIES

P.J.F. DAVIE

Davie, P.J.F. 1992 06 29: Revision of *Sarmatium* Dana (Crustacea:Brachyura: Sesarminae) with descriptions of three new species. *Memoirs of the Queensland Museum* **32**(1): 79-97. Brisbane. ISSN 0079-8835.

Sarmatium Dana, 1851, is revised and re-diagnosed. Crabs of this genus are primarily characterised by: carapace deeply vaulted; ocular peduncle swollen basally, cornea constricted and reduced; upper surface of palm of male cheliped bearing a series of transverse grooves separating transverse swollen ridges. *Sarmatium* is now considered to contain five species: *S. crassum* Dana, 1851; *S. germaini* (A. Milne Edwards, 1869); *S. striaticarpus* sp.nov.; *S. hegerli* sp.nov.; and *S. unidentatus* sp.nov. They are easily separated by the different patterns of ridges and grooves on the upper surfaces of the palm and carpus of the male cheliped. □*Crustacea, Brachyura, Grapsidae, Sesarminae, mangroves, Indo-West Pacific, new species.*

Peter J.F. Davie, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 3 February, 1992.

Sarmatium Dana, 1851, has a very confused history. Established for a single species *S. crassum* Dana, 1851, it was enlarged considerably by Tesch (1917) who included six other Indo-West Pacific species and two Atlantic species. Serène & Soh (1970: 398) pointed out that the two Atlantic species, *S. curvatus* H. Milne Edwards, 1837, and *S. pectinatus* H. Milne Edwards, 1853, are rightfully placed into the genus *Metagrapsus* H. Milne Edwards, 1853. Tesch (1917) had previously considered *Metagrapsus* as a junior synonym of *Sarmatium*. Features to separate the two genera were given by Serène & Soh (1970). The six Indo-West Pacific species placed in *Sarmatium* by Tesch: *S. integrum* A. Milne Edwards, 1873; *S. inermis* de Man, 1887; *S. indicum* A. Milne Edwards, 1868; *S. punctatum* A. Milne Edwards, 1873; *S. biroi* Nobili, 1905; and *S. fryatti* Tesch, 1917 (=*rotundifrons* A. Milne Edwards, 1869), are now all included in *Neosarmatium* Serène & Soh, 1970. Tesch (1917), following de Man (1891), considered *Sarmatium germaini* (A. Milne Edwards, 1869) to be a junior synonym of *S. crassum* but *S. germaini* was later shown to be a valid species by Serène & Soh (1971).

Serène & Soh (1971) considered *Sarmatium* to consist of two species, *S. crassum* and *S. germaini*. It is apparent however, after examining the larger amount of material available for the present study, that what Serène & Soh (1971) thought to be *S. crassum* from Singapore is in fact a new species. In addition, field work carried out in northern Australia has revealed two hitherto unknown species. With the five species here recognised, the genus concept for *Sarmatium* can now be much better understood.

Abbreviations used in the text are: AM, Australian Museum, Sydney; MNHN, Muséum national d'Histoire naturelle, Paris; ZRC, Zoological Reference Collection, National Museum of Singapore; NNM, National Natural History Museum, Leiden; QM, Queensland Museum, Brisbane; SMF, Senckenberg Museum, Frankfurt; USNM, United States National Museum, Washington; ZMG, Zoological Museum of Goetingen (collection housed at SMF); ZMH, Zoological Museum of Hamburg; ZMK, Zoological Museum Copenhagen. The descriptions for this paper were prepared using the DELTA computer system for generating taxonomic descriptions (Dallwitz & Paine, 1986).

Measurements given in the text are of the carapace breadth (measured at the widest point including lateral spines) followed by length. Leg segments were measured in a straight line to give maximum dorsal length and so are not always the maximum possible length, and this should be borne in mind when using the ratios. The exact limits of the width of the hind margin are also sometimes difficult to determine and in this work they were defined by the point at which the lateral carapace suture meets the rear margin. Gonopod terminology follows that of Sakai & Yatsuzuka (1979).

Sarmatium Dana, 1851

Sarmatium Dana, 1851a: 288; 1851b: 251; 1852: 357-8;

Kingsley, 1880: 212; Serène & Soh, 1970: 397; 1971: 237; Sakai, 1976: 664.

Sarmatium (in part): De Man, 1887: 659; Alcock, 1900: 426; Tesch, 1917: 213, 258; 1918: 115; Crosnier, 1965: 74.

Sesarma (*Sarmatium*) (in part): De Man, 1929: 111; Tweedie, 1936: 67.

TYPE SPECIES

Sarmatium crassum Dana, 1851.

DIAGNOSIS

Carapace sub-quadrate, slightly wider than long; greatest width behind exorbital angles; deeply vaulted, depth c.0.8- 0.9 × carapace width in males; regions moderately defined; anterolateral margins regularly convex; with 1-3 teeth behind the exorbital angle; front deflexed, c.0.35- 0.4 × carapace width, 0.5 × fronto-orbital width, pre-orbital teeth obsolete. Ocular peduncle swollen basally, cornea constricted and reduced. Basal segment of antennal peduncle with a well developed outer rounded tongue; antennal flagellum small and entering orbit. Basal antennular segment swollen. Inter-antennular septum narrow, 0.2- 0.3 × width of front. Median post-frontal lobes distinct, very broad, lateral lobes not clearly differentiated. Third maxilliped merus 0.7- 0.8 × length of ischium; merus longer than wide; outer margin convex; antero-external angle not produced; exopod narrow, barely visible in frontal view. Chelipeds subequal; upper surface of palm with a series of transverse grooves separating swollen ridges; outer surface of palm without median longitudinal row; dorsal surface of dactyl in males with at least one large, broad, chitinous tubercle, and some small pointed chitinous tubercles. Legs: merus anterior margin with an acute sub-distal spine, unarmed terminally; carpus with accessory carinae on upper surface. G1 long, reaching just past suture between sternites 2/3; moderately stout; completely calcified; palp obvious but not separated from stem, rounded, calcified; apical process corneous, strongly produced, straight; gonopore terminal or slightly displaced towards the dorsal surface. G2 short, relatively narrow, tapering, twisted, tip blunt. Male abdomen relatively narrow, third segment slightly the wider or sub-equal to first; first segment does not cover entire width of sternum between 4th pereiopods. Base of penis slightly calcified, just visible beneath setae adjacent to margin of third segment.

REMARKS

Sarmatium is separated from the two closest genera *Neosarmatium* and *Metagrapsus* by two major characters: 1, ocular peduncle swollen basally, cornea constricted and reduced; 2, upper surface of palm of male cheliped with a series of transverse grooves separating swollen ridges.

KEY TO THE SPECIES OF *SARMATIUM*

1. Outer ventral border of cheliped palm with a marked longitudinal ridge extending onto fixed-finger (even on juveniles and females); male cheliped with superior outer surface of palm bearing 7-8 relatively evenly spaced transverse grooves; dactylus with three large, strong chitinous tubercles on proximal half, followed by 17-18 small acute chitinous tubercles; carpus with a finely granular area distally, without trace of oblique fine striations. Maximum size c.28mm..... ..... *germaini* A. Milne Edwards, 1869

   Outer ventral border of cheliped palm and fixed-finger without a longitudinal ridge; male cheliped with superior outer surface of palm bearing less than 7 strong transverse grooves; dactylus variously armed, but not as above; upper face of carpus sometimes with oblique fine striations. Maximum size 28mm 2

2. Palm of male cheliped with 4 major transverse grooves on upper outer surface. Dactylus with four strong chitinous tubercles on proximal half. Maximum size c.25mm.....3

   Palm of male cheliped with transverse grooves not as conspicuous, but with a large, smooth or granular swelling occupying most of upper outer surface. Dactylus with only one major chitinous tubercle on proximal half. Maximum size 13-20mm.....4

3. Upper surface of carpus of cheliped with large patch of tiny, flattened, squamous granules behind articulation distally; these may be aligned into short fine rows near outer edge but never appear as transverse striations. Ridges and grooves on upper surface of palm all subparallel. First proximal tooth on dactyl of cheliped placed slightly distally from articulation.....*crassum* Dana, 1851

   Upper surface of carpus of cheliped with broad patch of c.25 long, fine, transverse striations

between articulation and spine of inner angle. Upper surface of palm with proximal most corrugated ridge separated from next broad groove by a triangular space. First proximal tooth on dactyl of cheliped placed almost on edge of proximal end .....*striaticarpus* sp.nov.

4. Male cheliped has dorsal margin of dactyl, with 1 large forwardly directed, chitinous tubercle on outer edge, proximally. Superior outer face of palm with 2-3 narrow, smooth grooves distally, followed by a deep concavity, and a large swelling back to the posterior margin, the distal slope of which is long and covered in well separated, medium sized, low round granules. Upper surface of carpus with 9 prominent transverse ridges distolaterally. Maximum size c.20mm.....*hegerli* sp.nov.

Male cheliped has dorsal margin of dactyl bearing a single, large, elongate, slightly oblique, medial tooth, proximally. Superior outer face of palm with very broad, deep, smooth, oblique depression, a very large rounded medial transverse swelling, and a narrow proximal band of seven very fine, long transverse ridges. Upper surface of carpus without transverse ridges. Maximum size c.13mm .....*unidentatus* sp.nov.

Sarmatium crassum Dana, 1851
(Figs 1A, 2, 3A-C)

Sarmatium crassum Dana, 1851b: 251; 1852: 358-9, pl. 23, fig. 1; H. Milne Edwards, 1853: 189; De Man, 1887: 651; Barnard, 1955: 28, fig. 9; Crosnier, 1965: 74-6, figs 121-124, pl. 5, fig. 1; McNeill, 1968: 78. - Serène & Soh, 1970: 397, 405 (name in list); Fishelson, 1971: 128, 130; Serène, 1973: 125-6; Hartnoll, 1975: 308, 318, 322-23; Holthuis, 1977: 174-5.

not *Sarmatium crassum*: Serène & Soh, 1970, pl. 4C, D; 1971: 237-40, fig. 2, pl. 2 [= *S. striaticarpus* sp. nov.]

?*Sarmatium crassum*: Nobili, 1899: 505; Alcock, 1900: 426-27; Tesch, 1917: 215.

TYPE SPECIMEN
Lost.

TYPE LOCALITY
Upolu, Samoa.

MATERIAL EXAMINED
NNM 24830, 1♂ (18.8×16.5mm), Melita Bay, Entedebiz, Dahlak Arch., L. Rode Iee, Eritrea, 14.4.1962, J.S.R.S. Expedition. MP-B10475, 1♂ (13.2×12.0mm), Nosy Be, Madagascar, mangroves, A. Crosnier. MP-B10474, 1♂ (12.8×11.5mm), Route de Ducos, 4km de Noumea, P. Fourmanoir, 7.8.1971. QM W16819, 1♂ (8.0×7.1mm) 1 imm. ♀ (8.7×7.4mm), Harmer Ck, far N Queensland , 11°50'S, 142°57'E, mouth of river in mudbank at low water, P. Davie & J. Short, 31.10.1990. QM W16829, 1♀ (18.5×15.7mm), same data as QM W16819. QM W6791, 2♂♂ (14.8×13.2; 21.1×19.3mm), Curtis I. nr Tide I., MEQ, 23°46'S, 151°15'E, 17.Dec.1975, P. Saenger, mud in *Rhizophora*. QM W6804, 1♂ (20.8×18.0mm), 2m from mouth of Auckland Ck, nr Gladstone, MEQ, 23°51'S, 151°14'E, 17.12.1975, P. Saenger, mud in *Avicennia*. QM W15228, 8♂♂ (21.5×19.2; 21.0×19.7; 19.5×17.3; 17.0×14.7; 17.1×15.2; 17.2×15.2; 13.9×12.5; 11.8×10.4mm), 4♀♀ (24.2×20.5; 21.4×18.2; 18.0× 15.2; 11.9×10.0mm), Calliope R. and Auckland Ck, Gladstone, MEQ, 23°51'S, 151°16'E, Queensland Electricity Commision Survey, 1974-1983, P. Saenger. QM W5387, 1♀ (15.6×13.4mm), Mary and Susan River Heads, Hervey Bay, SEQ, P. Davie, 25.7.1975. QM W5357, 1♂ (12.6×10.6mm), Moon Ck, Fraser I., SEQ, 25°11'S, 153°04'E, 21.7.1975, P. Davie, R. Timmins. QM W5382, 1♂ (19.1×17.3mm), Eli Ck, Hervey Bay, SEQ, 25°17'S, 152°49'E, 26.7.1975, P. Davie. QM W5351, 1♀ (17.6×15.1mm), Pulgul Ck, S of Urangan, Hervey Bay, SEQ, 25°19'S, 152°54'E, 19.7.1975, P. Davie. QM W5287, 1♀ (24.3×20.3mm), small branch of Serpentine Ck, SEQ, 27°24'S, 153°07'E, Sept 1972, B. Campbell et al. NNM Unreg., 1♂ (13.9×12.1mm), Snellius Exped., 16.9.1930, Bongao, Tanitawi, Sulu Arch. ZMK K4410, 1♀ (23.6×19.4mm), Tahiti.

DESCRIPTION

Carapace: c.1.1×broader than long in males, 1.2 in females. Fronto-orbital width c.0.75-0.85×carapace length. Carapace deeply vaulted; convex in both directions but only slightly from side to side. Depth c.0.8×carapace width (c.0.7 in females). Regions moderately defined; mesogastric well defined; cardiac distinct; intestinal distinct. Lateral margins subparallel; slightly concave. Anterolateral margins regularly convex; with two blunt teeth behind the exorbital angle; exorbital angle blunt, only slightly projecting. First anterolateral tooth similar in size to exorbital angle but with longer margin; second anterolateral tooth blunt; minute, almost obsolete. Front c.0.36-0.39×carapace width; c.0.5× fronto-orbital width; moderately deflexed; with shallow median emargination and bilobed; lateral

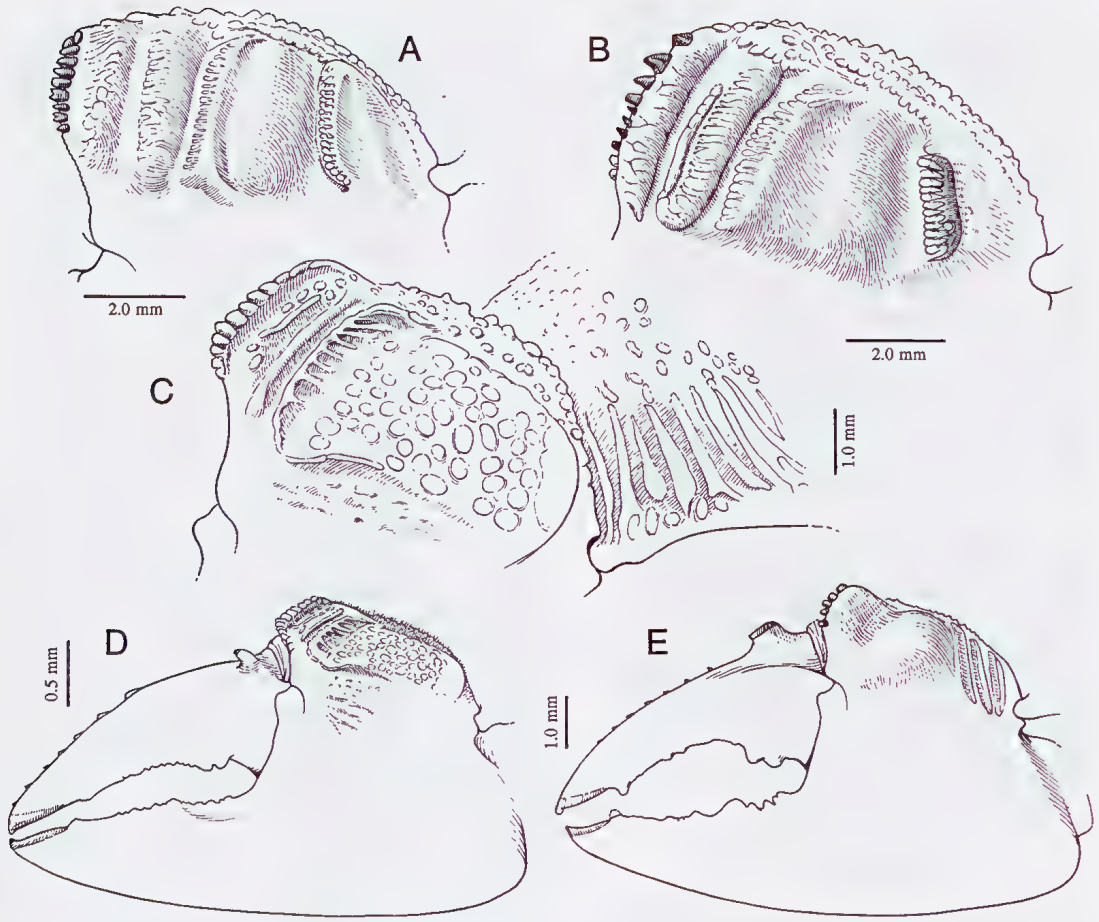

FIG. 1. A, *Sarmatium crassum* Dana, upper face of palm of♂ chela (QM W15228). B, *S. striaticarpus* sp.nov., upper face of palm of♂ chela (holotype, ZRC 1970.1.23.14). C,D, *S. hegerli* sp.nov., upper and outer faces of♂ chela (holotype, QM W9698). E, *S. unidentatus* sp.nov., outer face of male chela (holotype, AM P31822).

angles obtuse, blunt; pre-orbital teeth obsolete; lateral margins slightly diverging posteriorly. Post-frontal lobes distinct; median lobes distinctly broader than laterals; lateral lobes not clearly differentiated. Branchial ridges prominent forming a series of short broken granular striations; last continuous, parallel with posterolateral margin, and finishing over coxa of fourth walking leg. Posterior margin c.0.45-0.5 × carapace width. Carapace surface smooth, shining, punctate; setae arranged sparsely on branchial lines. Upper orbital border minutely granular; straight; inner angle rounded. Lower orbital border straight; evenly granular. Inner orbital tooth present; well developed; equilateral triangular, ocular peduncle swollen basally, cornea constricted and reduced. Basal segment of antennal peduncle with a well developed outer lobe in form of rounded tongue. Inter-antennular septum narrow; 0.22-0.24 × width of front.

Third maxilliped: Merus 0.7-0.8 × length of ischium. Suture between merus and ischium slightly sloping inward. Ischium inner margin microscopically granular. Palp articulates medially on distal margin of merus. Exopod narrow, barely visible in frontal view; flagellum normal.

Chelipeds: Subequal; large and robust. Merus posterior border with minutely granular striations; distinct subdistal spine; lower border granulate; anterior border convex, coarsely granulate; carpus with a small spine at inner angle; inner margin unarmed, striated, rounded, ventral-

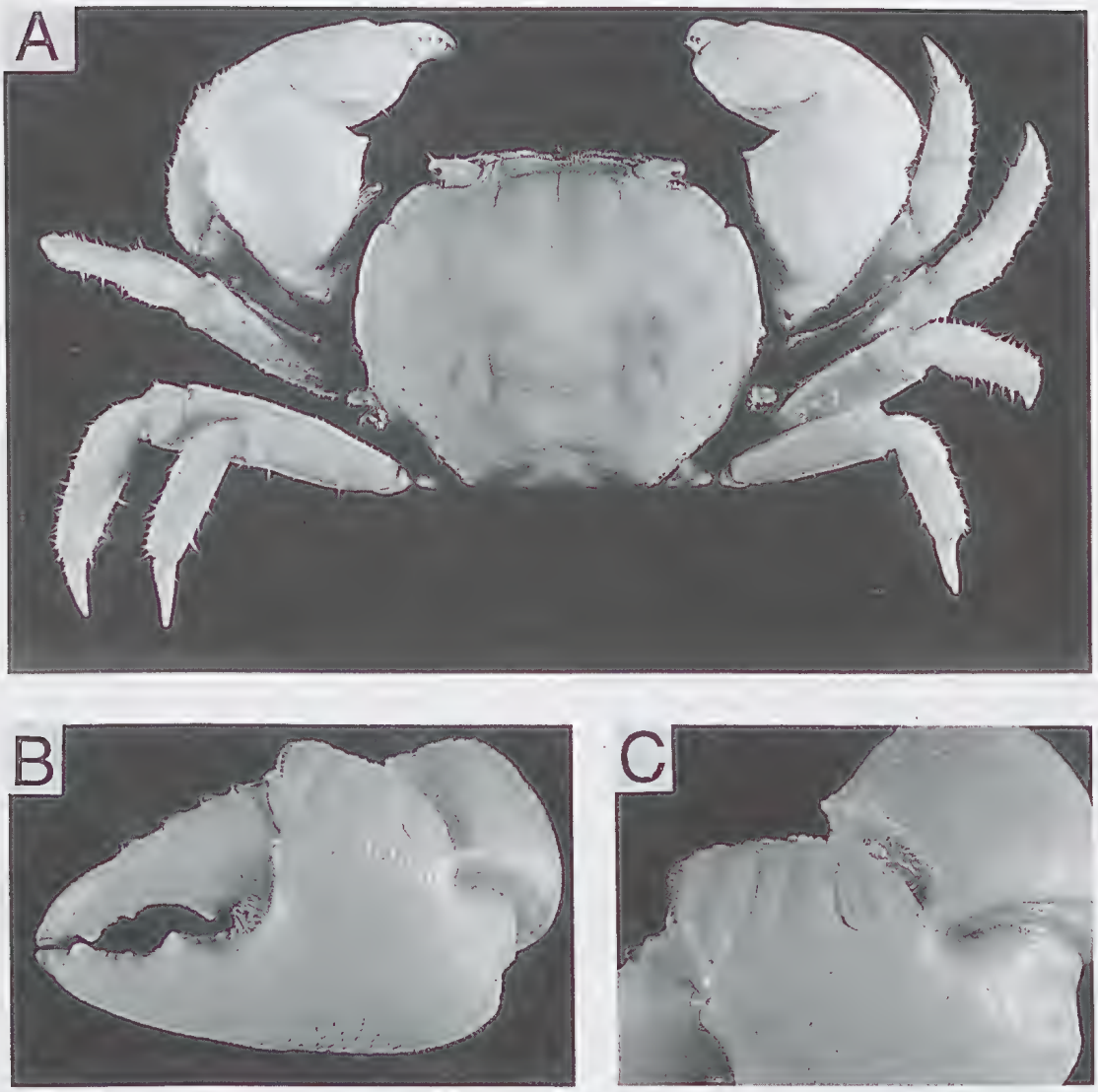

FIG. 2. *Sarmatium crassum*, ♂ (QM W15228). A, dorsal view. B, chela. C, upper surface of palm of chela. Scale line in mm.

ly with row of small granules and short proximal oblique crest bearing row of long setae; granules present on inner face of carpus just below inner angle; outer margin striated, with narrow patch of sparse, very short setae; upper surface microscopically striated proximally, smooth and wrinkled medially, behind articulation distally a large patch of tiny, flattened, squamous granules which become aligned into fine rows near outer edge. Palm upper surface with a series of transverse grooves separating swollen ridges, distal margin of upper surface of palm bearing row of 10-13 pectinated teeth along edge of articulation, proximal to this is a series of 6 broad, swollen, rounded ridges, relatively evenly separated, ridges 3/4 and 5/6 joined by low rim top and bottom; fourth ridge broader than others; fifth ridge low and with row of 15-20 granules along its lower distal edge; superior margin with a series of moderately large granules, but without conspicuous setation. Outer surface of palm smooth and punctate; without median longitudinal row; without a ventral ridge. Outer surface of palm naked, small patch of setae at base of fingers, fringe of setae at insertion of dactyl. Inner surface of palm with sparse large flat smooth granules,

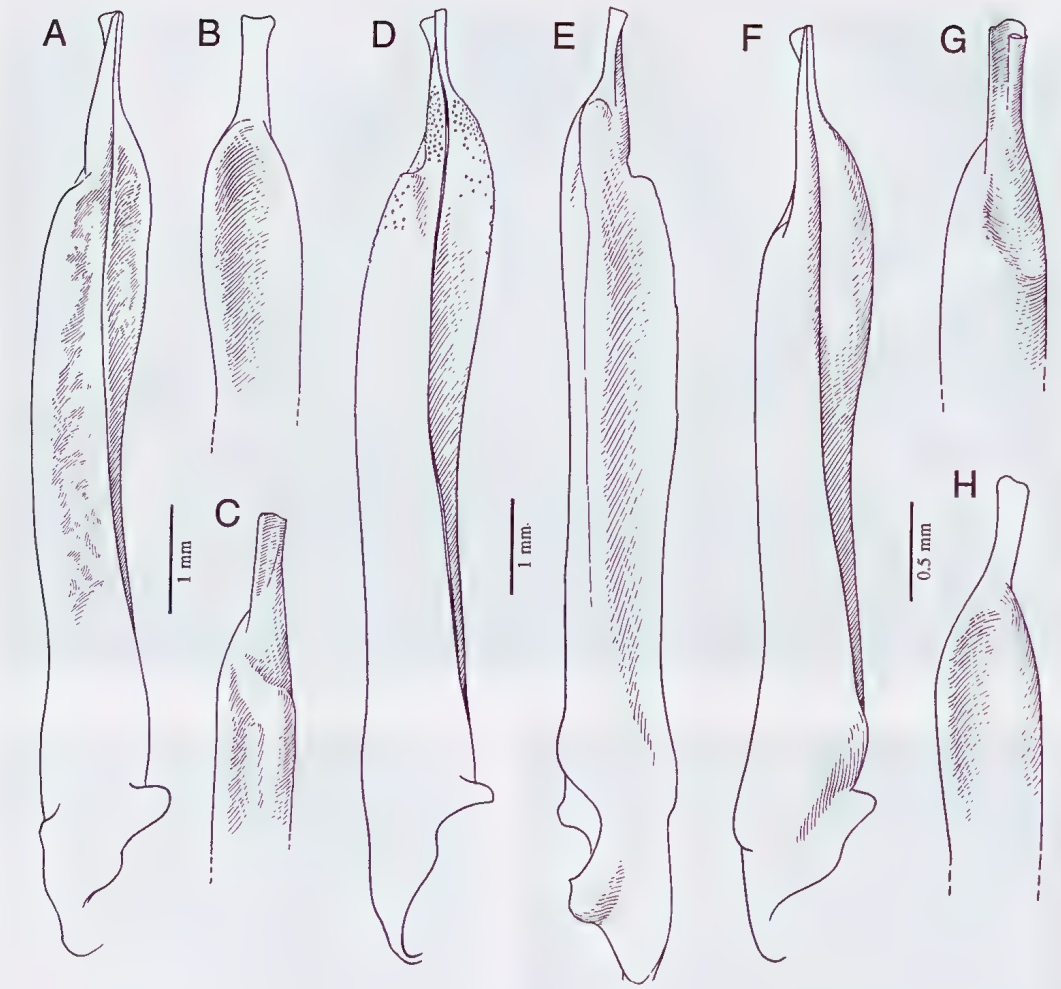

FIG. 3. Male first gonopods (setae removed). *Sarmatium crassum* Dana. A, abdominal view. B, C, lateral views of apex. *S. striaticarpus* sp.nov. D, abdominal view. E, sternal view. *S. hegerli* sp.nov. F, abdominal view. G, H, lateral views of apex.

largest and most conspicuous near gape, but not forming a strong vertical crest. Immovable finger slightly flattened on outer surface; moderately long. Length cutting edge c.0.45×length propodus in males (0.5 in females). Ventral border of chela straight, or slightly convex. Dorsal surface of dactyl of males bearing 4 large, broad, chitinous tubercles in proximal three-fifths, first set away from joint about same distance as to following tooth, a small patch of setae in the space; second tooth larger than first; third and fourth teeth largest, similar sized; teeth 1-4 set increasingly obliquely, highest towards outer face; followed in distal quarter by a row of 12-14 small closely set chitinous tubercles of even size. Fingers pointed; curved slightly inwards; a moderate gape between cutting margins in males.

Walking legs: Medium length; compressed and flattened; second pair slightly the longest, c.1.5-1.7×maximum carapace width. Third leg: merus c.2.4-2.6×as long as wide; carpus c.2.6-2.8×as long as wide; propodus c.2.3- 2.6×as long as wide. Dactyli about equal to length of propodi; slender and almost straight; terminating in acute chitinous tips. Propodus with an accessory carina on inferior proximal portion of upper surface. Meri of legs 1-3 with scattering of small distally directed prickles; dorsal and ventral borders of meri granulate. Setae short, predominantly on upper distal face of carpi, and on upper half of propodi, and continuing onto dactyli in thin rows.

Male abdomen: Relatively narrow; third segment slightly the widest. Slightly calcified base of penis adjacent to margin of third segment. Segments three-five slightly tapering. Width segment three 4.1-4.7 × length (relatively narrower in smaller males). Segment six not elongated; 1.45-1.6 × wider than long. Telson nearly subequal in length to segment 6; 1.25-1.5 × longer than wide (relatively longer in large males); evenly rounded.

Gonopods: G1 moderately stout; slightly curved. Inner-dorsal margin distally curved inward. Dorsal surface of stem flattened; completely calcified. Palp poorly developed, not separated from stem, large, broad, rounded, calcified. Outer dorsal margin of stem convex. Distal part of the stem broad but narrowing. Apical process present; corneous; strongly produced; straight. Gonopore slightly displaced towards the dorsal surface. Setae long, simple, dense, obscuring structural detail. G2 short, relatively narrow, tapering, twisted, tip blunt.

COLOURATION

Fawn-brown, chelipeds and legs biscuit-coloured with orange tinge (Barnard, 1955); carapace purple in life with yellow patches, thoracic legs yellow with purple patches (Crosnier, 1965).

DISTRIBUTION

With certainty from only the following localities: Samoa (Dana, 1851b, 1852); Durban Bay, South Africa (Barnard, 1955); Madagascar (Crosnier, 1965); Dar es Salaam, Tanzania (Hartnoll, 1975); Eritrea, Red Sea (Fishelson, 1971; Holthuis, 1977); Sulu Archipelago, Indonesia (present record); eastern Queensland, from Brisbane north to 11 50'S on Cape York (McNeill, 1968; and present records); New Caledonia (Serène, 1973); Tahiti (present record).

Questionably from: Sumatra (Nobili, 1906 - no diagnostic characters were given, so may also be atributable to *S. striaticarpus* sp.nov.); Nicobars (Alcock, 1900, single ♀ specimen); 'Pacific' (Tesch, 1917, single ♀ specimen).

HABITAT

In the mangroves (Crosnier, 1965; McNeill, 1968). 'An uncommon species in creek mangrove, where specimens were collected from the *Ceriops* and mixed zones' (Hartnoll, 1975). Mangroves; mouth of river in mudbank at low water; mud in *Rhizophora*; mud in *Avicennia* (present records).

REMARKS

Serène & Soh (1970) presented data and figures separating what they believed to be *Sarmatium crassum* from *S. germaini*. Unfortunately their *S. crassum* specimens represent a new species very closely allied to *S. crassum*, but differing in a number of distinctive characters (see later). The accurate identity of *S. crassum* is slightly problematic as, being a Dana species, the type was destroyed in the Chicago fire of 1871. This means that it is difficult to be absolutely certain what is the true *S. crassum*. After considering Dana's description, I consider the Asian specimens previously attributed to *S. crassum* to be the new species, and it is here named *S. striaticarpus*. *Sarmatium crassum* differs from *S. striaticarpus* on the following grounds:

1. The shape and disposition of the ridges and grooves on the upper surface of the palm are different. In *S. crassum* the ridges are all subparallel and this is evident in Dana's Fig. 1d; whereas in *S. striaticarpus* the proximal most corrugated ridge is separated from the next broad groove by a triangular space. Also there is a slight groove separating the distal row of pectinatious teeth in Dana's figure which is also true of my *S. crassum* material but not present in *S. striaticarpus*.

2. The first proximal tooth on the dactyl of the cheliped is placed slightly distally from the articulation in *S. crassum* and this also seems true of Dana's figure although it is not clear; in *S. striaticarpus* it is placed almost on the very edge of the proximal end.

3. So far, *S. striaticarpus* is only known for certain from vicinities north of the equator. To remove all doubt over the identity of *S. crassum* the erection of a neotype would be necessary. I am reluctant to do this because I have not seen specimens from the type-locality (Samoa). Although the Asian specimens certainly represent a new species (*S. striaticarpus*), slight reservations must remain about the identity of the specimens here referred to *S. crassum*. The shape of the male abdomen in Dana's figure differs a little from that of the present material, and it is difficult to ascertain if this difference is due to growth changes (Dana's specimen was quite small), inaccuracies in the figure, or if it does in fact represent a real difference at the species level. In this last case a new name would be required for the material here identified as *S. crassum*.

Sarmatium striaticarpus sp.nov. can further be separated from *S. crassum* on the following grounds: the small chitinous tubercles on the dis-

tal half of the dactyl of the cheliped are greater in number and more closely spaced in *S. crassum*; *S. striaticarpus* has a broad patch of c.25 long, fine, transverse striations, mostly continuous but some subdivided, on the upper surface of the cheliped carpus between the articulation and the spine of the inner angle, in *S. crassum* the upper surface is microscopically striated proximally, smooth and wrinkled medially, and with a large patch of tiny, flattened, squamous granules behind the distal joint, which become aligned into fine rows near outer edge.

Sarmatium striaticarpus sp.nov.
(Figs 1B, 3D,E, 4)

Sesarma (*Sarmatium*) *crassum*: Tweedie, 1936: 67-8.
Sarmatium crassum: Serène & Soh, 1970, pl. 4C, D; 1971: 237-40, fig. 2, pl. 2; Sakai, 1976: 664-5.
? *Sarmatium* sp. (aff. *S. crassum* Dana): Sakai, 1936: 173, text-fig. 7.

MATERIAL EXAMINED
HOLOTYPE: ZRC 1970.1.23.14, 1♂ (24.3×23.0mm), Johore Straits, C.L. Soh, 21.1.1970.
PARATYPES: USNM 73213, 1♀ (16.2×14.0mm), Iloilo, Panay I., Philippines, H.C. Kellers, U.S. Navy, April 1929, Ilo Ilo Eclipse Exped.

DESCRIPTION
Carapace: c.1.1×broader than long. Fronto-orbital width c.0.75×carapace length. Carapace deeply vaulted; evenly convex longitudinally, flat from side to side. Depth c.0.8-0.9×carapace width. Regions well defined; mesogastric well defined; cardiac distinct; intestinal indistinct, defined laterally by branchio-intestinal grooves. Posterolateral margins divergent posteriorly; moderately concave. Anterolateral margins regularly convex; cristate; with three blunt, forwardly directed teeth behind the exorbital angle (third reduced to trace only). Front c.0.36×carapace width; 0.5×fronto-orbital width; moderately deflexed; with a broad median emargination; lateral angles obtuse; pre-orbital teeth obsolete; lateral margins slightly diverging posteriorly. Medial post-frontal lobes very broad, well defined, laterals almost obsolete; without clumps of setae. No short ridge on first epibranchial tooth. Branchial ridges not prominent; relatively short. Posterior margin c.0.5×carapace width. Carapace surface smooth, shining, punctate; setae arranged sparsely on branchial lines. Upper orbital border evenly granular; straight and slightly oblique; inner angle rounded. Lower orbital border straight; smooth. Inner orbital tooth present; well developed; equilateral triangular. Antennal flagellum very small, entering orbit. Orbital hiatus open. Basal segment of antennal peduncle with an elongate, rounded outer lobe. Basal antennular segment moderately swollen. Inter- antennular septum c.0.23×width of front.

Third maxilliped: Merus c.0.7×length of ischium. Suture between merus and ischium slightly sloping inward. Ischium sub-triangular; inner margin smooth. Palp articulates near outer distal margin of merus. Exopod narrow, barely visible in frontal view; c.0.3×width of ischium; flagellum normal.

Chelipeds: Subequal; large and robust. Merus of male without stridulatory ridge; posterior border minutely granulate; distinct subdistal spine; lower border granulate; anterior border coarsely granulate medially. Carpus with a spine at inner angle; inner margin with narrow granular bead; granules present on inner face of carpus just below inner angle; outer margin with a series of smooth granular striations; between articulation and spine of inner angle is a broad patch of c.25 long, fine, transverse striations, mostly continuous but some subdivided. Palm upper surface with a series of transverse grooves separating swollen ridges; a distally swollen margin bearing row of 10-12 pectinated teeth along edge of articulation, largest near superior margin, minute distally; behind this a wide groove; then a ridge, itself subdivided by a narrow groove into a very narrow distal ridge and a wide proximal ridge; behind this a series of two very wide swollen ridges separated by a broad concavity, but both ridges connected by a narrow margin top and bottom; behind this a triangular depression with its apex dorsally, and then a pair of short, closely-set comb-like ridges. Outer surface of palm smooth and punctate; with slight depression at base of fixed finger; without ventral ridge. Outer surface of palm naked; with small patch of setae at base of fingers just fringing articulation. Inner surface of palm with a low granular vertical crest of 5-6 granules largest ventrally; and an oblique crest of about 6 large granules running from below vertical crest to upper part of fixed finger. Immovable finger slightly flattened on outer surface; moderately long; length cutting edge c.0.45×length propodus. Ventral border of chela slightly convex. Dorsal surface of male dactyl with 15-17 chitinous tubercles; 4 large, widely spaced tubercles, set obliquely, on the proximal half, becoming longer but no higher distally; in

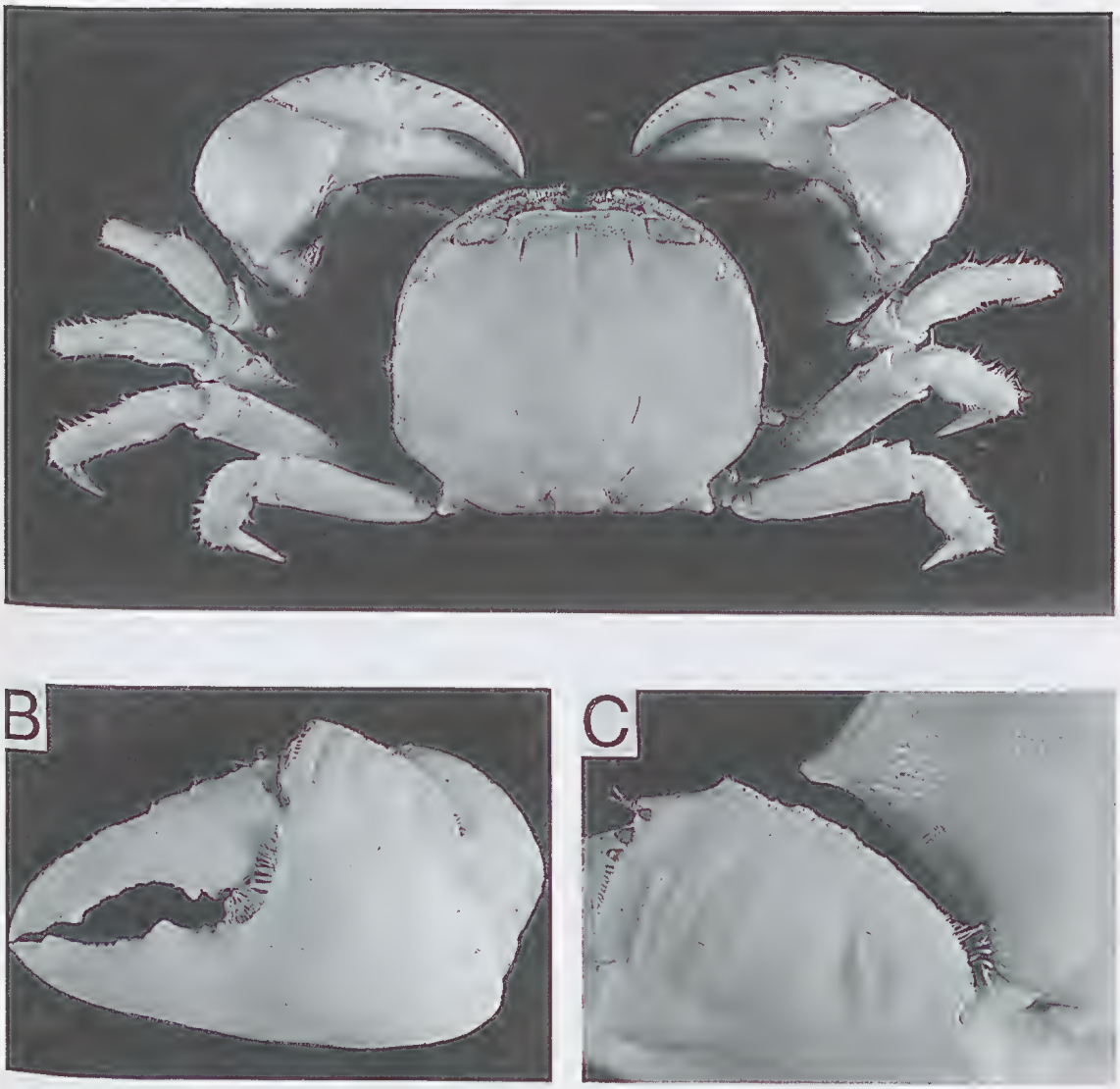

FIG. 4. *Sarmatium striaticarpus* sp.nov., ♂ (holotype, ZRC 1970.1.23.14). A, dorsal view. B, chela. C, upper surface of palm of chela. Scale line in mm.

distal half a row of 12 small closely set sharp tubercles, forwardly pointed, becoming minute distally; proximal portion of inner edge without distinct granules. Fingers pointed; curved inwards; a moderate gape between cutting margins.

Walking legs: Medium length; compressed; slender; first three pairs all of similar length but third pair slightly longest (c.1.7 × maximum carapace width). Third leg: merus c.2.8 × as long as wide; carpus c.2.6 × as long as wide; propodus c.2.6 × as long as wide; dactylus c.0.8 × length of propodus. Dactyli slender and slightly recurved; terminating in acute chitinous tips. Propodus with an accessory carina on inferior proximal portion of upper surface. Leg segments smooth, anterior margins minutely granular; fringed with short, soft, setae, also arranged in thin tufts in rows on anterior and posterior faces.

Male abdomen: Relatively narrow; third segment widest. First segment broad, only slightly narrower than third segment. Segments 3-5 slightly tapering. Width segment three c.4.3 × length. Telson longer than preceding segments, only slightly longer than sixth segment; c.1.4 × longer than wide; evenly rounded.

Gonopods: G1 moderately stout; slightly curved. Inner-dorsal margin evenly curved onto palp. Dorsal surface of stem flattened; completely

calcified. Palp well developed, separated from stem, large, narrow, rounded, calcified. Outer dorsal margin of stem convex. Distal part of stem broad but narrowing. Apical process present; corneous; strongly produced; straight. Gonopore displaced towards the dorsal surface. Setae long, simple, lying around corneous tip and apical part of stem obscuring structural detail. G2 short, evenly tapering, moderately twisted, apically pointed.

COLOURATION

Palm of the cheliped brownish red (Serène & Soh, 1971).

DISTRIBUTION

Singapore (Tweedie, 1936; Serène & Soh, 1971; present records); Southern Okinawa, Japan (Sakai, 1936, 1976); Philippines (present record). Relatively common in the mangroves of Singapore and Malaysia (Serène, 1973, referring to this species as *S. crassum*).

HABITAT

Mangrove swamp (Serène, 1973; Sakai, 1976; present records).

ETYMOLOGY

Named in reference to the characteristic striations on the upper surface of the carpus of the cheliped.

REMARKS

See 'Remarks' for *S. crassum*.

Sarmatium germaini (A. Milne Edwards, 1869)
(Figs 5, 6A-C)

Sesarma germani A. Milne Edwards, 1869: 28; De Man, 1887: 651; 1891: 51.

Sarmatium germaini: Serène & Soh, 1970: 397, 405; 1971: 238, fig. 1, pl. 1 (1-4); Soh, 1978: 11, pl. 4a.

MATERIAL EXAMINED

LECTOTYPE. MP-B3668 (Dry), 1♀ (15.0×16.6mm), Poulo Condore, South China Sea, coll. M. Germain.

PARALECTOTYPES. MP-B10472 (Dry), 1♂ (13.3×12.4mm), Poulo Condore, South China Sea, coll. M. Germain. (On the posterior portion of the carapace is written '428' and below this 'GS' in faded black ink - specimen is dry, carapace intact but left cheliped, various legs and abdomen are detached.) MP-B10473, 1♂, same collection data as B10472, badly broken.

OTHER MATERIAL. ZRC 1970.2.20.3, 1♂ (27.8×25.6mm), Johore Straits, Singapore, C.L. Soh, Feb. 1970. MP-B10471, 1♂ (26.0×24.4mm), Port Swettenham, Malaysia, coll. Sasekumar, 22.10.1968. MP-B21576, 1♀ (19.9×17.4mm), Serangoon R., Singapore, mangroves, 28.8.1965. MP-B21574, 1♂ (14.2×13.1mm) 1♀ (16.9×15.3mm), Johore Baharu, 1°28'N, 103°44'E, mangroves, 10.7.1965. QM W14858, 1♂ (27.9×26.8mm), Mandai Swamps, Singapore, 1°25'N, 103°45'E, 1985, D.H. Murphy. ZMG 191a, 2♀♀ (16.7, 21.8) 2♂♂ (20.4, 21.9mm), Mariveles, Aibuleit, Bohol, Philippines, coll. Semper, 1876. NTM Cr.003558, 1 juv. ♂ (7.8×7.2mm), Creek 'H', East Arm, Darwin, N.T., mangrove lined creek, mean low water, R. Hanley, 28.8.1985. NTM Cr.003555, 1♂ (11.6×10.7mm), same data as Cr.003558. NTM Cr.003714, 1♂ (13.7×12.4mm), Creek 'H', East Arm, Darwin, N.T., mangrove creek, 4m, R. Hanley, 31.10.1984. NTM Cr.003718, 1♀ (17.5×16.1mm), same data as Cr.003714. NTM Cr.001693, 1♂ (16.5×14.7mm), 12°34.2'S 130°56.3'E, Darwin, N.T., in mangroves, low water spring, R. Hanley, 17.5.1984. AM P31821, 1♀ (13.1×11.8mm), Andranangoo Ck, Melville I., 1.5km upstream, west bank, *Rhizophora* mudbank, D. Grace, 21.6.1975. SMF Unreg., 3♀♀ (21.7-25.8), Smith Ck, Cairns, Mangroves, M. Skinner, 5.6.1980. SMF Unreg., 1♀ (27.1×24.4mm), nr Australian Institute of Marine Science, Cape Ferguson, NEQ, M. Türkay, 11.6.1980. QM W12334, 3♂♂ (21.6×20.0; 22.6×21.2; 22.2×20.6mm), 1♀ (21.8×19.4mm), Townsville, NEQ, 19°16'S, 146°49'E. QM W8212, 1♀ (17.4mm), Murray R., NEQ, 18°01'S, 145°53'E, 23.5.1978, P.Davie, at burrow entrance at night 10m inland from bank. QM W12333, 1♂ (15.6mm), Cardwell, NEQ, 18°16'S, 146°01'E, K.Broadbent. QM W1100, 1♂ (16.5mm), Orpheus I., 18°4'S, 146°30' E, in mangrove area. QM W17485, 5♂♂ (10.0-19.5mm), 3♀♀ (9.1-15.2mm), Calliope R. and Auckland Ck, Gladstone, MEQ, 23°51'S, 151°16'E, Queensland Electricity Commision Survey, 1974-1983, P. Saenger. QM W17486, 1♀ (12.2×11.0mm), small branch of Serpentine Ck, SEQ, 27°24'S, 153°07'E, Sept 1972, B. Campbell et al.

DESCRIPTION

Carapace: c.1.1×broader than long. Fronto-orbital width c.0.8×carapace length. Carapace deeply vaulted; evenly convex longitudinally, flat from side to side. Depth c.0.9×carapace width. Regions moderately defined; mesogastric well defined; cardiac distinct; intestinal indistinct, defined laterally by branchio-intestinal grooves. Lateral margins slightly divergent posteriorly; slightly concave. Anterolateral margins regularly convex; usually with two blunt, forwardly

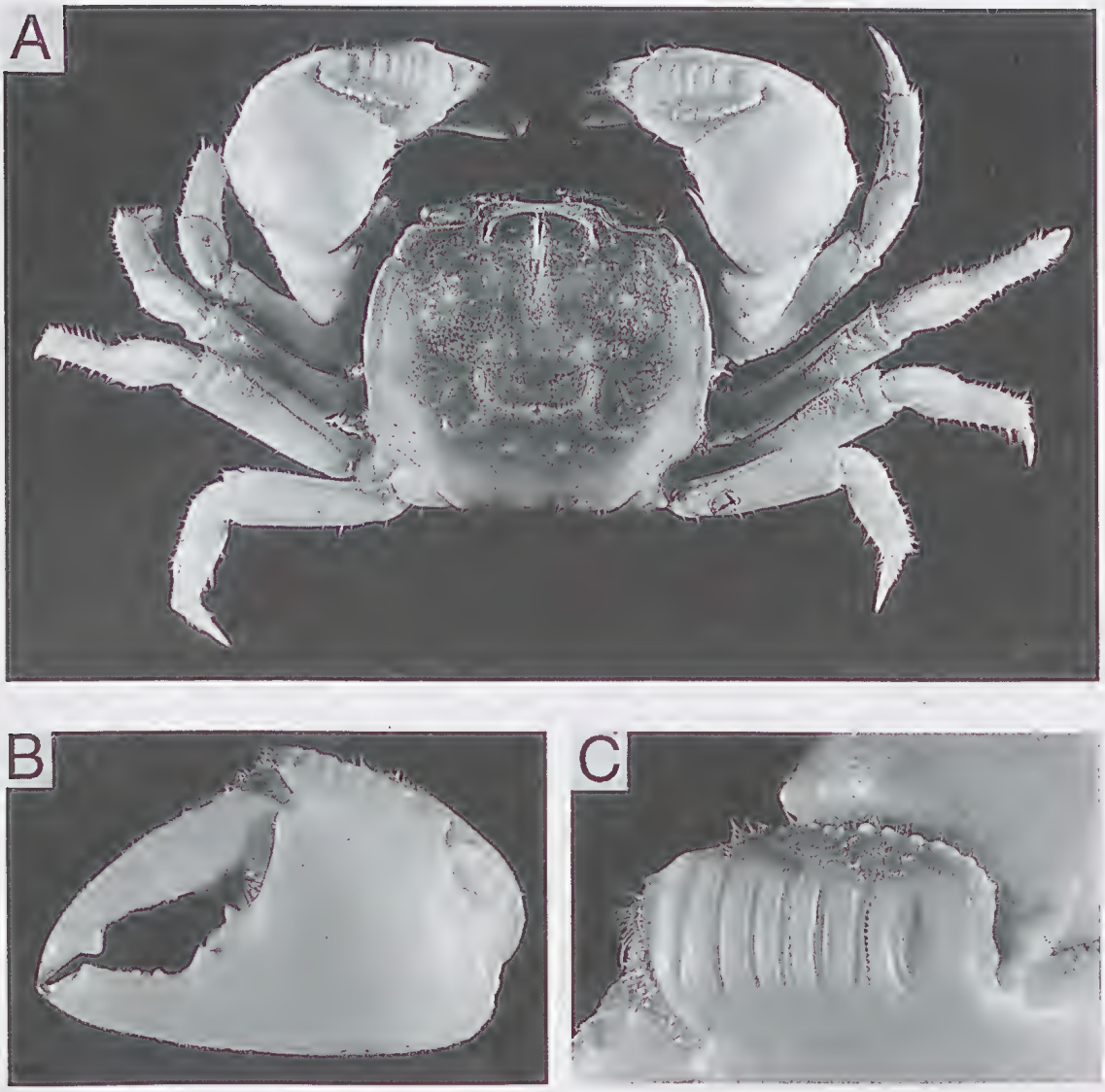

FIG. 5. *Sarmatium germaini* (A. Milne Edwards), ♂ (QM W14858). A, dorsal view. B, chela. C, upper surface of palm of chela. Scale line in mm.

directed teeth behind exorbital angle, a third tooth sometimes noticeable. Front c.0.4 × carapace width; 0.5 × fronto-orbital width; moderately deflexed; with broad median concavity; lateral angles obtuse; pre-orbital teeth obsolete; lateral margins slightly diverging posteriorly. Post- frontal lobes medially well defined, laterally indistinct; without clumps of setae. Branchial ridges moderately prominent; relatively short. Posterior margin c.0.5 × carapace width. Carapace surface smooth, shining; wrinkled and punctate posteriorly; setae arranged sparsely on branchial lines. Upper orbital border evenly granular; with slight median convexity; inner angle rounded. Lower orbital border straight; evenly granular. Inner orbital tooth present; well developed; equilateral triangular. Basal segment of antennal peduncle with broad and rounded outer lobe. Inter-antennular septum narrow; 0.25-0.3 × width of front.

Third maxilliped: Merus c.0.8 × length of ischium. Suture between merus and ischium horizontal. Ischium sub- triangular; inner margin smooth. Palp articulates near outer distal margin of merus. Exopod narrow; 0.4 × width of ischium; flagellum normal.

Chelipeds: Subequal; large and robust; merus

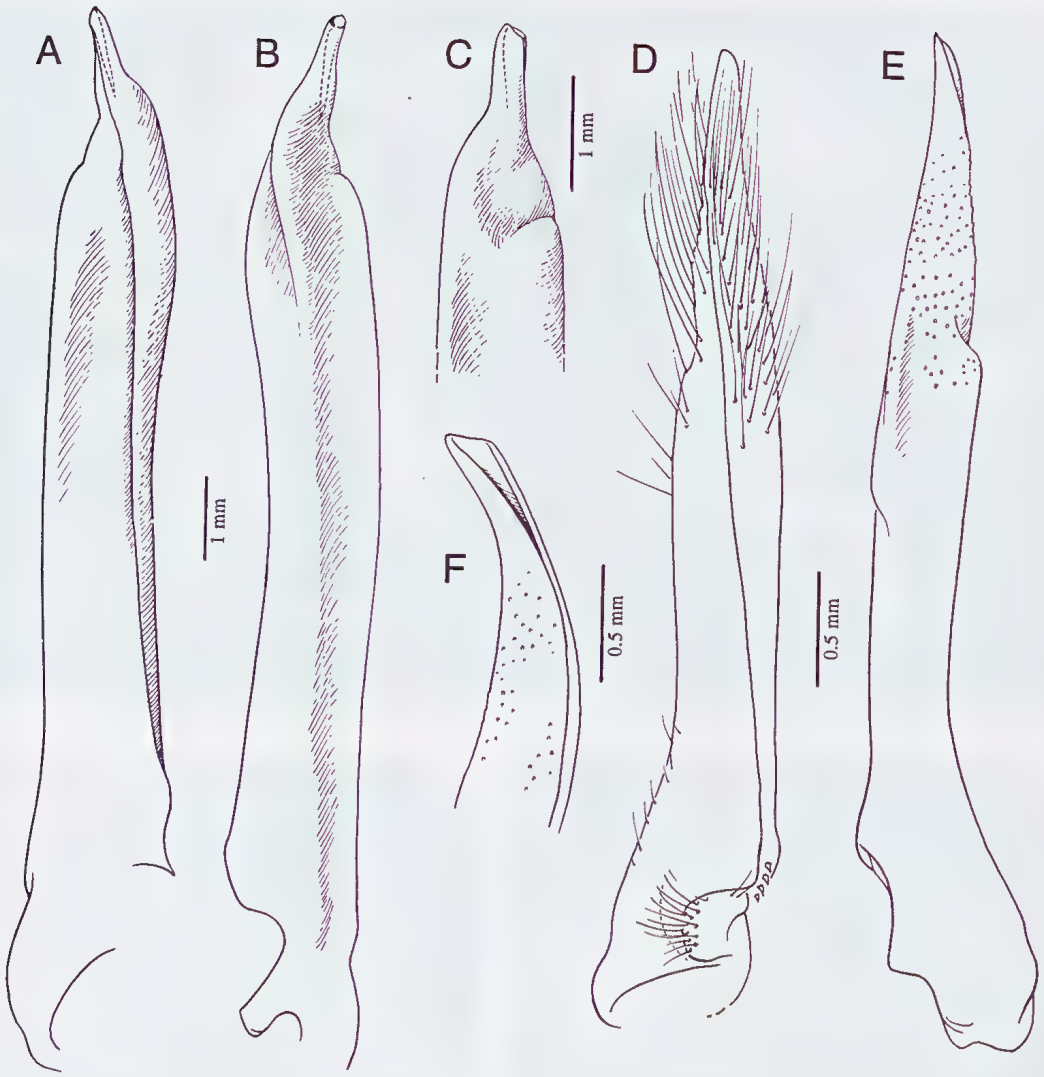

FIG. 6. Male first gonopods (setae removed, except for D). *Sarmatium germaini* (A. Milne Edwards) (QM W14858). A, abdominal view. B, sternal view. C, lateral view of apex. *S. unidentatus* sp.nov. (holotype, AM P31819). D, abdominal view. E, sternal view. F, lateral view of apex.

with posterior border minutely granulate; without distinct subdistal spine; lower border granulate; anterior border sparsely granulate, slightly coarser medially; carpus with a broad tooth at inner angle; tubercles present on inner face of carpus just below inner angle, 1 or 2 ventrally on vertical crest; outer margin smooth, wrinkled, upper medial surface behind articulation with a broad patch of small flattened vesicular tubercles. Palm upper surface with a series of transverse grooves separating swollen ridges: upper distal margin behind articulation with a row of 14-17 blunt chitinous tubercles, slightly larger towards inner end; behind this a series of 8 transverse swollen ridges, first 7 of similar shape evenly spaced, third to seventh subequal in width, slightly narrower than first and second; behind seventh, a much broader sulcus separating a much broader, proximal transverse swelling; ridges 3/4, 5/6, 7/8 narrowly connected top and bottom, more-or-less obviously; ridges 3,5, and 7 with a line of punctations on distal edge, deeper on 5, very deep on 7 so as to form a series of gutters with a prominent granule at the base of each gutter; behind transverse ridges superior border with large rounded granules. Outer surface of palm smooth

and punctate; without median longitudinal row. Ventral ridge extends to tip of fixed finger, less distinct distally, very prominent behind fixed finger, extends less than halfway towards proximal end. Outer surface of palm naked except for fringe of short setae around dactyl articulation; with a patch of 'fur' on superior margin behind transverse ridges. Inner surface of palm smooth; without a vertical crest. Immovable finger slightly flattened on outer surface; moderately long. Length cutting edge c.0.4-0.5×length propodus. Ventral border of chela convex, straight in small specimens. Dorsal surface of dactyl bearing 3 large chitinous tubercles in proximal half, set obliquely; followed immediately by 17-18 small acute chitinous tubercles. Fingers pointed; slightly curved inwards; a wide gape between cutting margins.

Walking legs: Medium length; cylindrical; slender; second pair slightly the longest, c.1.7×maximum carapace width. Third leg: merus c.2.3-2.5×as long as wide; carpus c.2.6-2.7×as long as wide; propodus c.2.2- 2.3×as long as wide; dactylus c.0.95×length of propodus. Dactyli slender and slightly recurved; terminating in acute chitinous tips. Propodus without short accessory carina on inferior proximal portion of upper surface. Meri of legs 1-3 with a scattering of small sharp prickles on outer surface; leg segments fringed with short setae, setae arranged in thin tufts in rows on anterior and posterior faces.

Male abdomen: Relatively narrow; third segment the widest. First segment broad, only slightly narrower than third segment. Segments three-five slightly tapering, each with slightly concave margins. Width segment three c.4.3×length. Telson length subequal to sixth segment; c.1.4×longer than wide; evenly rounded.

Gonopods: G1 moderately stout; curved. Inner-dorsal margin evenly curved onto palp. Dorsal surface of stem flattened; completely calcified. Palp poorly developed, not separated from stem, large, narrow, rounded, calcified. Outer dorsal margin of stem convex. Distal part of the stem narrow. Apical process present; corneous; strongly produced; straight. Gonopore terminal. Setae long, simple, lying around corneous tip and apical part of stem obscuring structural detail. G2 short, evenly tapering, moderately twisted, apically pointed.

Colouration

Greenish brown with reddish tinge on legs (A. Milne Edwards, 1869); palm of the cheliped yellowish light brown (Serène & Soh, 1971).

Distribution

Poulo Condore Island, Vietnam, South China Sea (type locality, A. Milne Edwards, 1869); Singapore and Malaysia (Serène & Soh, 1971, and present record); Hong Kong (Soh, 1978); Philippines (present record); northern Australia - from Brisbane to Darwin (present records).

Habitat

In the mangroves and nearly always out of the water (A. Milne Edwards, 1869). Mangrove lined creek at mean low water; *Rhizophora* mudbank; at burrow entrance at night 10m inland from creek bank (present records).

Remarks

A. Milne Edwards (1869) did not specifically designate a holotype but he gives the measurements for only a single specimen of 17×16mm, and does not mention its sex. From his description of the 'six ou sept très-petits bourrelets obliques et parallèles' on the chela, one might think that he examined a male, but these ridges are also present, albeit indistinctly, on the female. His note on habitat - that this species was collected almost always out of the water - does suggest that he was given more than one specimen to examine. De Man (1891) says, 'I was enabled to study a typical male specimen of *Ses. Germani* of the Paris Museum', but he does not give measurements. Serène & Soh (1971) state, 'The senior author ... was able to re-examine the holotype of *S. germaini* in the Paris Museum (April 1970); it is a dry female and not a male as indicated by De Man (1891).' The decision is taken here to designate the female as the lectotype - its measurements do not precisely conform to those given by A. Milne Edwards, but they are very near. There are also two dry male specimens at the Paris Museum, MP-B10472-3, and one of these was presumably the specimen examined by De Man. A relatively modern label identifies them as being collected by M. Germain from Poulo Condor, but no original labelling has been preserved. The specimens (one is little more than a series of fragments) are indeed *S. germaini* as defined here, and by Serène & Soh (1971), however they are both much smaller than the measurements given by A. Milne Edwards. They are considered, along with the female discussed above, to have been syntypes, and are thus designated here as paralectotypes.

The spelling of the species name was justifiably emended by Serène & Soh (1971) as the species was clearly intended to be named after its collector, R. Germain, and can thus be considered an 'incorrect original spelling' under Article 32(c) of the International Code of Zoological Nomenclature (1989, Third Edition).

Sarmatium hegerli sp.nov.
(Figs 1C,D, 3F-H, 7)

MATERIAL EXAMINED

HOLOTYPE: QM W9698, 1♂ (19.6×17.4mm), East Alligator R., Kakadu National Park, N.T., burrow in moist bank of drainage channel (K836), P. Davie, May 1980.

PARATYPES: QM W9699, 1♂ (9.9×8.7mm), East Alligator R., Kakadu N.P., N.T., edge of drainage channel in *Ceriops/Avicennia* stand with a thick *Aegilaitis* understory, (T6Q2) P. Davie, 19.6.1982. QM W9700, 1♂ (12.4× 10.8mm), East Alligator R., Kakadu N.P., N.T., open *Sonneratia* forest, very soft sloppy mud, (T6Q4) P. Davie 19.6.1982. QM W9701, 1 juv. (6.6×6.1mm), East Alligator R. Mouth, Kakadu N.P., N.T., low open *Avicennia/Aegilaitis* scrub, moist but firm substrate, some succulent saltmarsh plants, crab from shaded raised burrow entrance very near surface, (T5Q1), P. Davie, 16.6.1982. QM W9702, 1♂ (10.8 ×9.2mm), East Alligator R., Kakadu N.P., N.T., open *Sonneratia* forest, very soft sloppy mud (T6Q5), P. Davie, 19.6.1982. QM W9703, 4♀♀ (12.4×10.4; 12.1×9.6 (bopyrid infection); 10.9×9.0; 10.1× 8.5mm) 1♂ (13.6×11.9mm), East Alligator R., Kakadu N.P., N.T. (Site 27), P. Davie, May 1980. QM W9704, 1♂ (13.2 ×12.0mm), Middle Arm, Darwin, N.T., in burrow under rock rear boat ramp, firm mud, tidally inundated, salinity 32 ppt at low water, P. Davie, 29.6.1982. NTM Cr.001826, 1♂ (15.8×14.3mm), locality not supplied. NTM Cr.003068 1♂ (24.6×11.8mm), Creek 'H', East Arm, Darwin Harbour, 12°33.2'S, 130°56.3'E, mangroves, mean low water, R. Hanley, 1.7.1985.

DESCRIPTION

Carapace: c.1.1×broader than long in males, c.1.2 in females. Fronto-orbital width c.0.8×carapace length (0.9 in females). Carapace deeply vaulted; convex anteriorly, almost flat from side to side. Depth c.0.8×carapace width. Regions moderately defined; mesogastric well defined; cardiac distinct; intestinal indistinct, defined laterally by branchio-intestinal grooves. Lateral margins subparallel; slightly concave. Anterolateral margins regularly convex; with three blunt teeth behind the exorbital angle; second small but obvious, third minute almost obsolete. Exorbital angle blunt, rounded, not projecting. First anterolateral similar in size to exorbital angle but with longer margin. Front c.0.36- 0.39×carapace width; c.0.5×fronto-orbital width; moderately deflexed; with shallow median emargination; lateral angles rounded; pre-orbital teeth obsolete; lateral margins slightly diverging posteriorly. Median post-frontal lobes distinct, distinctly broader than laterals which are not clearly differentiated. Branchial ridges prominent as a series of short broken granular striations; last continuous, parallel with posterolateral margin, and finishing over coxa of fourth walking leg. Posterior margin c.0.5×carapace width. Carapace surface smooth, shining, punctate. Setae in short tufts over entire surface, less prominent on cardiac and intestinal regions. Upper orbital border minutely granular; straight; inner angle rounded. Lower orbital border straight; evenly granular. Inner orbital tooth present; well developed; acute equilateral triangular. Basal segment of antennal peduncle with well developed, elongate, rounded outer lobe. Inter-antennular septum narrow; 0.22-0.24×width of front.

Third maxilliped: Merus c.1.4×length of ischium. Ischium inner margin microscopically granular. Palp articulates medially on distal margin of merus. Exopod narrow, barely visible in frontal view; flagellum normal.

Chelipeds: Subequal; large and robust; merus with posterior border minutely granulate; with distinct subdistal spine; lower border minutely granulate; anterior border sparsely granulate, with a few large rounded granules medially on convexity; carpus with a spine at inner angle; inner margin minutely granular, rounded, ventrally with minutely granulate crest and a long proximal oblique ridge bearing row of long setae; granules present on inner face of carpus just below inner angle; outer margin striated, bearing thick band of short setae; upper surface smooth and sparsely granulate, with distinctive area of 9 prominent ridges and 8 grooves, running transversely along outer distal half behind joint. Palm upper surface with a series of transverse grooves separating swollen ridges: distal margin of upper surface of palm raised, with a series of 4-8 short, broad, truncated, chitinous teeth; proximal to this a series of 3 ridges separating 3 narrow smooth grooves, or sometimes the first ridge low and uneven and followed by area of small smooth granules, and then the other two arced ridges; on proximal slope of last ridge is a series of short ridges and grooves, longest towards upper mar-

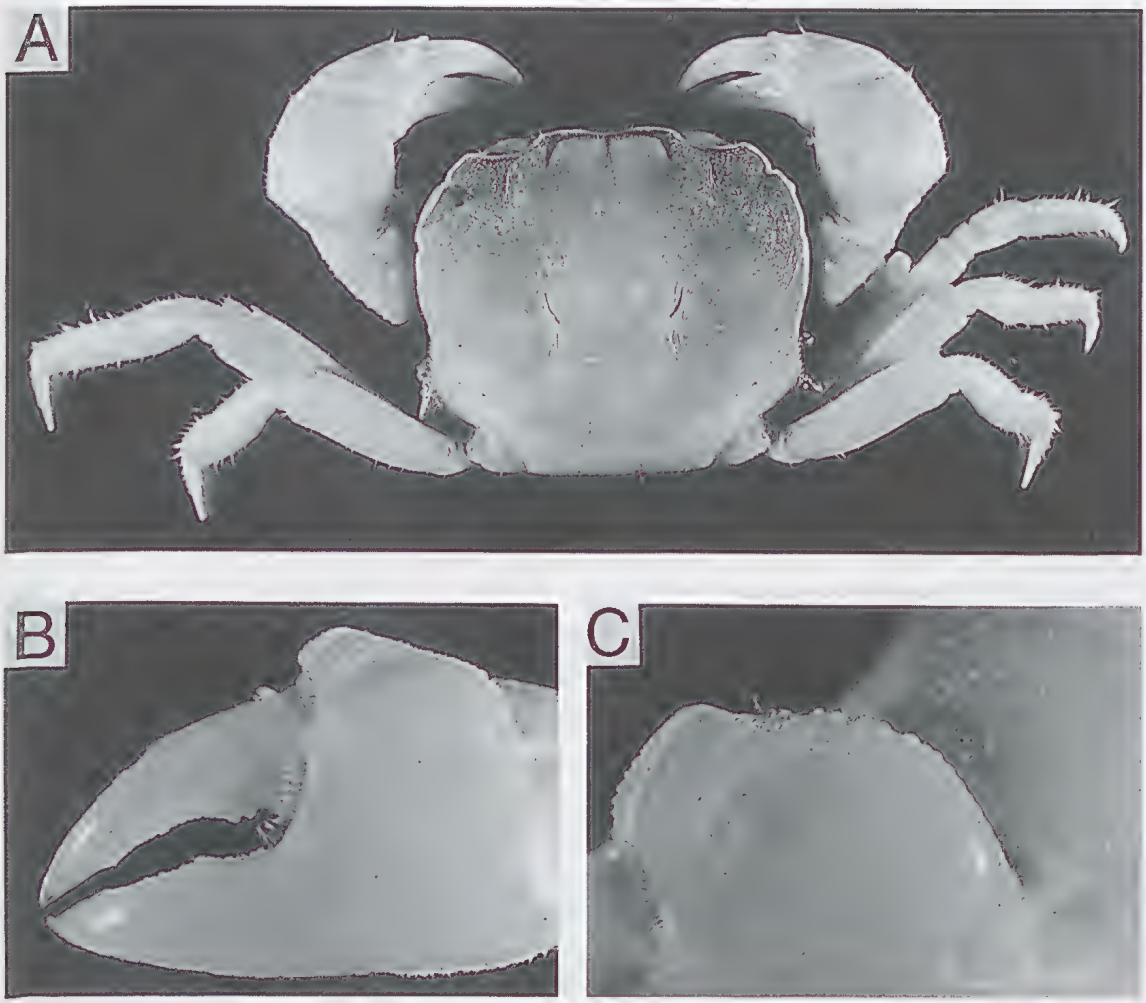

FIG. 7. *Sarmatium hegerli* sp.nov., ♂ (holotype, QM W9698). A, dorsal view. B, chela. C, upper surface of palm of chela. Scale line in mm.

gin; behind this a very broad deep concavity, and then a large swelling back to posterior margin, the distal slope of which is long and covered in well separated, medium sized, low round granules; superior margin with large rounded granules and short setae. Outer surface of palm smooth; without median longitudinal row; without a ventral ridge. Outer surface of palm naked except for fringe of setae at insertion of dactyl, and a small patch ventro-proximally behind joint and as a triangular patch proximally on ventral face. Inner surface of palm smooth; without vertical crest but with a few very low rounded tubercles, almost indistinguishable. Immovable finger rounded on outer surface; without ventral ridge; moderately long. Length cutting edge c.0.45-0.49× length propodus. Ventral border of chela straight, or slightly convex. Dorsal surface of dactyl with 1 large forwardly directed, bluntly pointed, chitinous tubercle proximally near joint on outer edge of superior margin; 5-6 additional chitinous tubercles commencing c.two-fifths distance towards tip; first large, oblique, truncate; second smaller of same form; third also similar but very small, distal 2-3 minute and reducing distally, last tubercle situated well before tip; thick triangular patch of setae proximally on upper surface near joint. Fingers pointed; slightly curved inwards; a narrow gape between cutting margins in largest male, no gape in smaller males.

Walking legs: Medium length; compressed; second pair slightly the longest, c.1.3-1.5× maximum carapace width. Third leg: merus c.2.4-2.7× as long as wide; carpus c.2.5- 2.7× as long

as wide; propodus c.2.3 × as long as wide. Dactyli about equal to length of propodi; slender and slightly recurved; terminating in acute chitinous tips. Propodus with an indistinct accessory carina on inferior proximal portion of upper surface. Meri of legs 1-3 with scattering of small distally directed prickles; dorsal and ventral borders of meri granulate. Setae short, covering anterior and posterior faces of carpi and propodi, and distal upper margins of meri; continue on to proximal half of dactyli in thin rows.

Male abdomen: Relatively narrow; third segment the widest, subequal with first. Segments three-five tapering. Width segment three c.4.25-4.9 × length, relatively narrower in smaller males. Segment six not elongated; 1.25-1.35 × wider than long. Telson longer than preceding segments, only slightly longer than segment 6; 1.4- 1.5 × longer than wide; evenly rounded.

Gonopods: G1 moderately stout; slightly curved. Inner-dorsal margin distally curved inward. Dorsal surface of stem flattened; completely calcified. Palp poorly developed, not separated from stem, large, broad, triangular, calcified. Outer dorsal margin of stem convex. Distal part of the stem broad but narrowing. G1 apical process corneous; strongly produced; straight. Gonopore slightly displaced towards the dorsal surface. Setae short, simple, obscuring structural detail. G2 short, relatively narrow, tapering, twisted, tip blunt.

Sternum: Thick covering of setae between insertion of telson and mouth frame.

Habitat

Mangroves; burrows in riverbanks and banks of drainage channels; moist to very sloppy mud; not restricted to a particular mangrove zone. One burrow, apparently belonging to this species had a raised entrance, but this does not seem typical.

Distribution

Only known from Northern Territory, Australia.

Etymology

Named for Mr Ed Hegerl, director of the Australian Littoral Society, and one of Australia's leading marine conservationists. Someone I have followed into very many, very muddy places.

Remarks

The key provided here separates *Sarmatium hegerli* sp.nov. from all other known species of *Sarmatium*. The pattern of grooves and ridges on the upper surface of the palm of the cheliped; the shape, number and position of the cheliped dactylar tubercles; and the male first gonopod are distinctive.

Sarmatium unidentatus sp.nov.
(Figs 1E, 6D-F, 8)

Material Examined

Holotype: AM P31822, 1♂ (12.5 × 10.9mm), Nungbalgarri Ck, N.T., 2.5km upstream, west bank, D. Grace, 27.7.1976.

Paratype: AM P31819, 1♂ (11.7 × 10.4mm), Liverpool R., N.T., 14.3km upstream, amongst debris on mud floor in *Rhizophora* mangrove forest, D. Grace, 30.1.1975.

Description

Carapace: c.1.15 × broader than long. Fronto-orbital width c.0.85 × carapace length. Carapace deeply vaulted; convex in both directions, only slightly from side to side. Depth c.0.8 × carapace width. Regions moderately defined; mesogastric well defined; cardiac distinct; intestinal distinct. Lateral margins slightly divergent posteriorly; slightly concave. Anterolateral margins regularly convex; with two blunt teeth behind the exorbital angle. Exorbital angle blunt, rounded not projecting. First anterolateral tooth similar in size to exorbital angle but with longer margin. Second anterolateral tooth minute. Front c.0.4 × carapace width; c.0.5 × fronto-orbital width; moderately deflexed; with shallow median emargination; lateral angles quadrate, rounded; pre-orbital teeth obsolete; lateral margins sub-parallel. Median post-frontal lobes distinct, distinctly broader than laterals; lateral lobes not clearly differentiated. A series of short broken granular branchial striations; last continuous, parallel with posterolateral margin, and finishing over coxa of fourth walking leg. Posterior margin c.0.5 × carapace width. Carapace surface smooth, shining, punctate. Setae arranged sparsely on branchial lines. Upper orbital border minutely granular; straight; inner angle rounded. Lower orbital border straight; evenly granular. Inner orbital tooth present; well developed; bluntly triangular. Basal segment of antennal peduncle with a well developed elongate, rounded outer lobe. Basal antennular segment swollen. Inter- antennular septum narrow; 0.22-0.24 × width of front.

Third maxilliped: Merus c.1.35 × length of ischium. Ischium inner margin granular. Palp articulates medially on distal margin of merus.

FIG. 8. *Sarmatium unidentatus* sp.nov., ♂ (holotype, AM P31819). A, dorsal view. B, chela. Scale line in mm.

Exopod narrow, visible proximally and distally in frontal view but mostly hidden; flagellum normal.

Chelipeds: Subequal; large and robust; merus with posterior border minutely striated; without distinct subdistal spine; lower border granulate; anterior border convex, coarsely granulate; carpus with inner angle granular; inner margin rounded, ventrally with row of minute granules and short proximal crest bearing row of long setae; granules present on inner face of carpus just below inner angle; outer margin striated, bearing rows of short dark setae; upper surface smooth and shiny distally, microscopically striated proximally. Palm upper surface with a series of transverse grooves separating swollen ridges: distal border of upper surface of palm with prominent crest bearing 5-6 short, broad, truncated, chitinous teeth; proximal to this a very broad, deep, smooth, oblique depression; then a very large medial transverse swelling; then a series of seven very fine, long transverse ridges ending near proximal margin of upper border; first six ridges joined top and bottom to form 3 pairs; superior margin distinctly granular, and lacking setation. Outer surface of palm smooth; without median longitudinal row; without a ventral ridge. Outer surface of palm naked except for fringe of setae at insertion of dactyl. Inner surface of palm sparsely granular, mostly smooth; with a low vertical crest of c.3 granules. Immovable finger rounded on outer surface, or slightly flattened on outer surface proximally; without ventral ridge; moderately long. Length cutting edge c.0.45 × length propodus. Ventral border of chela concave at base of fixed finger, bearing a shallow longitudinal depression. Dorsal surface

of dactyl tuberculate, bearing a pronounced slightly oblique, elongate proximal tooth, truncated and capped with chitin; a small patch of setae proximal to this tooth; distally followed by a broad gap and then a series of evenly spaced very small, acute, forwardly directed, chitinous tubercles, becoming minute distally and finishing at about three-quarters length of finger. Fingers pointed; curved inwards; a wide gape between cutting margins.

Walking legs: Medium length; compressed; second pair the longest, c.1.6-1.7 × maximum carapace width. Third leg: merus c.2.7 × as long as wide; carpus c.2.4- 2.5 × as long as wide; propodus c.2.5 × as long as wide. Dactyli about equal to length of propodi; slender and recurved; terminating in acute chitinous tips. Propodus without distinct accessory carina on inferior proximal portion of upper surface. Meri of legs 1-3 with scattering of small distally directed prickles; meri granular on superior margins; minutely striated over upper half. Setae very short and sparse on anterior halves of meri; thicker on upper halves of carpi, particularly along accessory ridges; also present on propodi on superior border and on both anterior and posterior faces, but disappearing distally; most obvious on anterior legs.

Male abdomen: First 3 sements subequal in width in holotype but third segment the widest in paratype. Segments three-five tapering, markedly from 3-4, then moderately. Width segment three c.4.6-4.8 × length. Segment six not elongated; c.1.8 × wider than long. Telson longer than preceding segments; c.1.3 × longer than wide; evenly rounded.

Gonopods: G1 moderately stout; slightly sigmoid. Inner-dorsal margin distally curved inward. Dorsal surface of stem flattened; completely calcified. Palp poorly developed, not separated from stem, small, narrow, rounded, calcified, situated c.two-thirds distance towards tip. Outer dorsal margin of stem convex. Distal part of the stem narrow. G1 apical process present; corneous; strongly produced; stout not markedly narrower than distal part of stem; straight. Gonopore terminal. Setae long, simple, lie around tip, mostly distal to palp. G2 short, relatively narrow, tapering, tip blunt.

Sternum: Thick covering of setae between insertion of telson and mouth frame.

HABITAT

Amongst debris on mud floor in *Rhizophora* mangrove forest.

DISTRIBUTION

Only known from Nungbalgarri Ck and Liverpool R., Northern Territory, Australia.

ETYMOLOGY

Named for the single pronounced slightly oblique, elongate, proximal tooth on the dactyl of the cheliped which is diagnostic.

REMARKS

The key provided here separates *Sarmatium unidentatus* sp.nov. from all other known species of *Sarmatium*. The pattern of grooves and ridges on the upper surface of the palm of the cheliped; the shape, number and position of the cheliped dactylar tubercles; and the male first gonopod are distinctive.

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THE RARE SHRIMP, *PHYLLOGNATHIA CERATOPHTHALMA* (BALSS), DISCOVERED IN MORETON BAY. *Memoirs of the Queensland Museum 32(1): 98:-* A collection of Crustacea was made by SCUBA diving at Myora, North Stradbroke Island, Moreton Bay. One particularly striking species excited interest, and proved to be the rare shrimp *Phyllognathia ceratophthalma* Balss. The Myora coral community occurs as a shallow (1-3m), narrow reef, with six coral species (Lovell, 1989). It is unusual within Moreton Bay in having large plates of *Acropora digitifera* (Dana). These grow attached to loose rubble on a muddy-sand substrate, which means they are easily overturned to sample the associated fauna. This small reef has a high diversity of invertebrates, including species which are more typically expected on outside reefs. This is possibly because during times of flooding when the rest of the Bay is subject to severe freshwater dilution, circulation patterns within the Bay cause a pooling of undiluted seawater along the northern side of Stradbroke Island. The reef also lies just to the side of the main channel leading in and out of the Bay, so recruitment from open coastal waters, and the warm southerly flowing East Australian Current, can be expected. See Bruce (1991) for full synonomy.

Phyllognathia ceratophthalma (Balss, 1913)

Hymenocera (?) *ceratophthalma* Balss, 1913: 236.
Phyllognathia ceratophthalma: Borradaile, 1915: 206; Bruce, 1991: 267-269, fig. 28.

Material Examined: QM W17487, 1 ♂ (8.0 mm cl (including rostrum)) & 1 ♀ (11.0 mm cl), Myora, Moreton Bay, 2m, in hole in base of *Acropora digitifera* plate, 14.4.1992, P. Davie.
Remarks: Bruce (1991) provided a modern figure and description of this apparently rare shrimp. The present specimens have an identical colour pattern to that described by Bruce (1991) but differ in having a translucent white/cream, rather than yellow-brown, background colour. Despite being known since 1913, and despite widespread use of SCUBA for underwater collecting over the past 25 years, this strikingly coloured shrimp is known from only four previous records: Satsuma, Japan, the type locality (Balss, 1913); Maldive Islands (Borradaile, 1915); Lizard Is., northern Great Barrier Reef; New Caledonia (Bruce, 1991). The present record is a significant southerly range extension.

On the tenth day after capture, the female was seen to release larvae from under her abdomen although her ovigerous state had not been previously apparent from casual observation. 25 first stage zoeae were released, and a further 16 were found in a 'brood pouch' formed by the broad, overlapping pleopods. This species is reproductively a K-strategist, with a small number of large eggs. It probably can maintain a breeding population at this southerly, subtropical locality. The first zoeae will be described elsewhere. Facilities were not available to rear them to later stages.

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Peter J.F. Davie, Queensland Museum, PO Box 3300, South Brisbane, Q. 4101, Australia; 1 May, 1992.

FIG. 1: *Phyllognathia ceratophthalma* (Balss, 1913), Queensland Museum W17487.

CYMBASTELA, A NEW GENUS OF LAMELLATE CORAL REEF SPONGES

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Seven species of lamellate, stalked sponges from Australasian waters are referred to a new genus, *Cymbastela* gen.nov. Six species from tropical, predominantly coral reef habitats: *C. stipitata* (Bergquist & Tizard) (type species) and *C. vespertina* sp.nov., both from NW Australia, *C. concentrica* (Lendenfeld) and *C. coralliophila* sp.nov. both from the Great Barrier Reef, Queensland, *C. marshae* sp.nov. from the Houtman-Abrolhos Is, Western Australia, and *C. cantharella* (Lévi) from New Caledonia). Another species is recorded from temperate South Australian waters (*C. notiaina* sp.nov. from the Gulf of St Vincent). All the species conformed to the existing interpretation of *Pseudaxinyssa* Burton, but they are referred here to *Cymbastela* since all are substantially different from the type species of *Pseudaxinyssa, A. tethyoides* Kirkpatrick. *Pseudaxinyssa* is synonymized with *Axinyssa* Lendenfeld. The seven species of *Cymbastela* are primarily differentiated by their spicule length and geometry, axial and extra-axial skeletal development, growth form, lamella thickness and live colouration. Four species are sympatric over part of their range in tropical Australia, whereas three species have more restricted, allopatric distributions in temperate Australia and the western Pacific Ocean. ☐ *Pseudaxinyssa, Axinyssa, Cymbastela, new genus, new species, Porifera, Axinellidae, taxonomy, biogeography, Australasia.*

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No formal revision of the complete order Axinellida has yet been published, even though for many years it has been recognized these marine sponges were polyphyletic (Bergquist & Hartman, 1969). Recent work on several families within the Axinellida, using a phylogenetic framework, has gone some way towards redistributing some of these taxa amongst other existing orders. Families considered so far (with their affinities as suggested by particular authors), are Axinellidae (Halichondrida; Van Soest et al., 1990), Desmacellidae (Poecilosclerida; Van Soest, 1984), Hemiasterellidae (Hadromerida; Hooper, 1986; Voultsiadou-Koukoura & Van Soest, 1991), Rhabderemiidae (Poecilosclerida; Hooper, 1990), and Raspailiidae (Poecilosclerida; Hooper, 1991). However, it is not yet clear whether the concept of an order Axinellida should be abandoned completely, or retained and restricted to one or few families. Additional, non-morphological data is required to confirm or refute these ideas (discussion in Hooper et al., 1992), and until such is available none of the above assignments can be completely endorsed.

Axinellidae is undoubtedly the most difficult of all the families of Axinellida to interpret. The original conception of the family, basically corresponding to the old subfamily Axinellinae of Lendenfeld (1889), with major additions by Hallmann (1916) and de Laubenfels (1936), included genera with an 'axinellid skeletal plan' consisting of a condensed axial core with diverging plumose or plumo-reticulate extra-axial branches. This definition stands today (e.g. Hartman, 1982), even though nearly half of the 50 nominal genera included in the family have skeletal structures other than axinellid (e.g. evenly reticulate - *Reniochalina*; sinuous - *Rhaphoxya*; dendritic - *Acanthella*; thickly encrusting/leptoclathrid - *Fasubera*). In such cases, genera with atypical skeletal structures were included in Axinellidae because their spicule geometries were similar to those with axinellid skeletons. However, recent biochemical evidence indicates that the family contains several distinctly heterogenous groups of genera (Bergquist & Hartman, 1969; Hooper et al., 1992).

A recent revision of halichondriids by Van Soest et al. (1990), based primarly on morphological characters, suggested that genera of Axinellidae could be redistributed into three existing families (Axinellidae, Desmoxyidae and Halichondriidae) and a new family (Dictyonellidae). Van Soest et al. (1990) referred these four families to the order Halichondrida, and although we do not presently support or refute this ordinal placement, we agree that for the Axinellidae at least, there is a pressing

need for a re-evaluation of the major morphological characters used to distinguish taxa within the Axinellidae, including the relative importance of these characters as reliable indicators of phylogenetic affinity.

It is difficult in many cases to assign species of Axinellidae to genera with complete assurance, as there are few morphological characters with clear importance at the supraspecific level. Unlike most groups within Poecilosclerida, for example, Axinellidae lack any unique or diverse spicule geometries, and lack microscleres which could provide clues on affinities between genera. Thus, the major problem preventing resolution of the supraspecific taxonomy of Axinellidae is the difficulty or inability to define autapomorphies and, furthermore, there is disagreement in the interpretation of the relative importance of the few existing morphological characters that do occur in the group - in particular spicule shape and skeletal organization. Biochemical evidence may provide more objective information on the affinities of the numerous genera presently included in the family, but the few data available are not entirely clear (Hooper et al. 1992): there are, in many cases, no obvious morphometric characters that correlate consistently with generic groupings based on chemotaxonomic data (see Hooper et al., 1992). The 'axinellids' are one group of Porifera that require rigorous genetic study.

The existing subdivision within Axinellidae, resting solely on morphological features, concerns the skeletal architecture, presence or absence of a specialised ectosomal skeleton, and morphology and diversity of structural megascleres. The curvature and geometry of megascleres, however, is thought to vary considerably within a particular species groups, and confuse the interpretation of interrelationships between species even further. This problem was first identified by Dendy (1905), who noted that oxeas may become strongyles or even styles, and curved or sinuous strongyles, once considered apomorphic for genera such as *Acanthella*, reappear throughout the family.

Consequently, it is not surprising that there are many genera of Axinellidae that presently contain heterogenous assemblages of species, particularly the large groups of *Phakellia*, *Acanthella*, *Axinella*, to each of which numerous species have been assigned. A similar situation exists for *Pseudaxinyssa*, and although it contains only eight nominal species - prior to the present work - some of these are obviously quite different from the type species. Lévi (1983) first stated that *Pseudaxinyssa* was probably polyphyletic, and this was recently reiterated by Van Soest et al. (1990). The present paper re-evaluates *Pseudaxinyssa*, returns its type species and several other described species to *Axinyssa*, and creates a new genus to receive several described species and a number of new species mainly from tropical Australian coral reef habitats.

METHODS

Preparation of material for light microscopy and scanning electron microscopy (SEM) is described elsewhere (Hooper, 1991). Abbreviations used in the text are as follows: AM, Australian Museum, Sydney; BMNH, The Natural History Museum, London; CMNZ, Canterbury Museum, Marine Invertebrate collection, Christchurch; MNHN LBIM, Muséum National d'Histoire Naturelle, Laboratoire de Biologie des Invertébrés Marins et Malacologie, Paris; NCI Q66C-, US National Cancer Institute shallow water collection program (Australian Institute of Marine Science, Townsville, contract) - primary material in USNM, duplicates/fragments in NTM and QM; NTM, Northern Territory Museum, Darwin; ORSTOM, Institute Français de Recherche Scientifique pour le Developpement en Cooperation, Noumea; PIBOC, Pacific Institute of Bio-organic Chemistry, Far Eastern Scientific Centre, Academy of Sciences of the USSR, Vladivostok; QM, Queensland Museum, Brisbane; SMF, Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington; ZMB, Zoologisches Museum für Naturkunde an der Humboldt-Universität, Berlin.

SYSTEMATICS

Family AXINELLIDAE Ridley & Dendy

Axinyssa Lendenfeld, 1897

Axinyssa Lendenfeld, 1897:116; Burton, 1931:349; Van Soest et al., 1990:25.

Axinomimus de Laubenfels, 1936:163; Van Soest et al., 1990:27 (type species *Axinella paradoxa* Ridley & Dendy, 1886:482 [by monotypy]; holotype BMNH 1887.5.2.68).

Pseudaxinyssa Burton, 1931:350; Van Soest et al., 1990:27 (type species *Axinyssa tethyoides* Kirkpatrick, 1903:245 [by original designation]; holotype BMNH 1902.11.16.25, schizotype MNHN LBIM DCL298).

Not *Pseudaxinyssa*, sensu Bergquist & Tizard, 1967: 190; Lévi, 1983:719.

TYPE SPECIES

Axinyssa topsenti Lendenfeld, 1897:116 (by monotypy) (holotype ZMB 2971, schizotype BMNH 1908.9.24.145).

DIAGNOSIS (emended)

Massive, frequently subspherical, sometimes lobate or lobate-digitate growth forms, often with an apical cloacal cavity or fistulose surface conules; surface with prominent, regularly spaced conules; choanosomal axial skeleton open plumose, dendritic or vaguely radiating tracts of larger oxeas, without axial compression, with poorly developed spongin fibres; fibres cored by larger oxeote megascleres; subectosomal extra-axial skeleton plumose, plumo-reticulate, ascending to surface, without obvious spongin fibre component; mesohyl usually with abundant collagenous spongin; specialised ectosomal skeleton may be present in the type species, or absent, consisting of tufts of smaller oxeas perched on peripheral choanosomal skeleton, protruding through surface, forming surface conules; megascleres oxeas or modified oxeas, one or two sizes.

REMARKS

Lendenfeld (1897:116) created the genus *Axinyssa* for a single species, *A. topsenti* Lendenfeld, which had a vaguely plumose, ascending choanosomal skeleton composed of multispicular tracts of large oxeas, with smaller stylote oxeote spicules in brushes on the surface. These choanosomal spicule tracts and smaller ectosomal brushes protrude through the surface for a short distance, producing characteristic microconules. There is no distinctive, compressed core in the skeleton (termed 'axial condensation'), although there is differentiation between the axial and extra-axial regions. Several other species were subsequently described and included in *Axinyssa* (Kirkpatrick, 1903; Topsent, 1906; Wilson, 1925).

Burton (1931) created *Pseudaxinyssa* for two species previously assigned to *Axinyssa* - the type species *A. tethyoides* Kirkpatrick (1903), and *A. gravieri* Topsent (1906). He also included a previously undescribed species, *P. tenuispicula* Burton (1931) from Natal. All three species differed from *Axinyssa* sensu stricto in lacking a specialised ectosomal skeleton of smaller styloid oxeas. They were closer to *Axinella* in their skelatal structure, but had only oxeas as megascleres (*Axinella* usually has styles and oxeas, or only styles, although at least one anomolous oxea-bearing species is also known [see below]). Van Soest et al. (1990) noted that a specialised ectosomal skeleton, such as that seen in *A. topsenti*, commonly occurs within many axinellids and, as such, it may not be a reliable or even valid taxonomic character when used above the species level. We provide further evidence to support this conclusion in the present work, (i.e. *Cymbastela coralliophila* sp.nov. having a specialised ectosomal skeleton), supporting the proposal that *Axinyssa* and *Pseudaxinyssa* (s.s.) should be merged.

Pseudaxinyssa, as defined by Burton (1931), were massive sponges, without strong differentiation between the axial and extra-axial skeletons, and without any evidence of axial condensation. The type species *Axinyssa tethyoides* (Kirkpatrick) is subspherical, with fistulose, usually blind surface papillae, with large oxeas between 530-790μm long scattered between skeletal tracts and forming a branching reticulate, non-compressed, undifferentiated skeletal architecture (i.e. no distinct axial and extra-axial components). However, the subsequent addition of two stalked, cup-shaped sponges from the Indo-west Pacific, *Pseudaxinyssa stipitata* Berquist & Tizard (1967) and *P. cantharella* Lévi (1983), did not fit at all with the original conception of the genus. These two species had compressed-reticulate axial skeletons, with diverging plumose (or plumo-reticulate) extra-axial skeletons, and spongin fibres were reasonably well developed. Both groups of species were similar to *A. tethyoides* only in having diverging tracts of oxeas near the periphery of the skeleton, whereas in other features they were quite different. Therefore, it is proposed here to include these anomolous stalked, predominantly cup shaped species in a new genus.

Following from Van Soest et al.'s (1990) revision of *Axinyssa* and our own observations on various museum specimens, 13 species may be referred to the genus, most from the tropical oceans (also indicating known geographic distributions, and material we have examined):

A. aculeata Wilson (1925:445) (Philippines; none).

A. ambrosia (de Laubenfels, 1934:14) (Puerto Rico; none).

A. aplysinoides (Dendy, 1922:39) (Cargados Carajos, Amirante, Seychelles; none).

A. digitata (Cabioch, 1968:229) (Roscoff; none).

A. fenestratus (Ridley, 1884:464) (Arafura Sea; holotype BMNH 1882.2.23.255).

A. gravieri Topsent (1906:563) (Red Sea; specimen of Lévi (1965:15), MNHN LBIM DCL327L).

A. paradoxa (Ridley & Dendy, 1886:482) (Tristan de Cunha Is; none).

A. pitys (de Laubenfels, 1954:178) (Palau Islands; holotype USNM 23103).

A. radiata (Lévi & Lévi, 1983:968) (New Caledonia; paratype MNHN LBIM DCL 2955).

A. tenuispicula (Burton, 1931:350) (Natal; none).

A. tethyoides Kirkpatrick (Natal; holotype BMNH 1902.11.16.25).

A. topsenti Lendenfeld (Adriatic; holotype ZMB 2971).

A. valida (Thiele, 1899:12) (Moluccas; ? paratype SMF 1821).

Another species exists in the MNHN collections, identified as a new species of *Pseudaxinyssa* by Claude Lévi (pers.comm.) ('holotype' MNHN LBIM DCL1497) from Anborombe, Africa (M. A. Crosnier stn CRO 69), and it too should be included in *Axinyssa*. The affinities of the remaining species which have been included in *Pseudaxinyssa* at one time or another are as follows:

P. cantharella Lévi (1983:719) (New Caledonia) belongs to the new genus described below.

P. stipitata Bergquist and Tizard (1967:189) (northern Australia) also belongs to the new genus described below.

P. tricalyciformis (Bergquist, 1970:15) (holotype CMNZ Mar. Inv. 3/63), a replacement name for *Axinella lamellata* Bergquist (1961:188) (preoccupied), from the Chatham Islands, was referred to *Pseudaxinyssa* by Bergquist & Tizard (1967:190). It has oxeas, some with styloid modifications, forming a condensed axial skeleton and plumose extra-axial skeleton, and is returned to *Axinella*. Discrepancies in dates of referral and description of that species are a consequence of delayed publication of the 1970 paper, which was completed in 1966 (Bergquist, 1970:4).

Following Van Soest et al.'s (1990) revision of the 'halichondrid' axinellids *Axinyssa* was referred to the family Halichondriidae Vosmaer, as emended by them, in having vague, ill-defined spicule tracts, with a high ratio of spicules to spongin. By comparison, 'true' members of the Axinellidae have ordered, axially condensed, extra-axially plumo-reticulate skeletons. The type species of *Pseudaxinyssa*, *A. tethyoides* fits well with the emended definition of Halichondriidae (see Figs 1-2), and a redescription of *A. tethyoides* is provided here for comparative purposes with the new genus described below.

Axinyssa tethyoides Kirkpatrick
(Figs 1-2)

Axinyssa tethyoides Kirkpatrick, 1903: 245-6, pl. 5, fig.12, pl.6, fig.8a,b.; Van Soest et al., 1990:27, fig.18.

Pseudaxinyssa tethyoides; Burton, 1931:350.

Material Examined
Holotype: BMNH 1902.11.16.25: Cone Point, Natal, South Africa, 68m depth. Schizotype: MNHN LBIM DCL298.

Substrate and Depth Range
Broken shell substrate.

Geographical Distribution
Known only from the type locality.

Description
Shape: Subspherical, massive growth form, 64mm diameter, with slightly flattened basal region (point of attachment) (Fig. 1A).

Surface features: Detachable, relatively fragile skin, covered with numerous small papillae, 2-5mm long, 1-2.5mm diameter, most erect, fistulose, but few open at the apex. When open, diameter of oscule approximately 1mm.

Colour: Live colouration unknown, mottled black and dark brown in ethanol.

Texture: Firm, barely compressible consistency, easily crumbled.

Ectosome: Membraneous, without specialised skeleton, with moderate quantities of detritus within heavy organic matrix, occasionally with spicules from peripheral choanosomal skeleton protruding through surface, corresponding to surface papillae (Fig. 2B).

Choanosome: Skeleton branching reticulate, open-meshed (mesh diameter 140-320μm), without trace of axial condensation or differentiation between axial or extra-axial regions. Skeletal tracts pauci- or multispicular, 80-170μm wide, composed of tightly bound oxeas, without spongin fibres, bound together within heavy collagenous mesohyl (Fig. 1B). Near periphery skeletal tracts diverge to surface, protruding through ectosome slightly or not at all.

Spicules: Oxeas of single size class, long, robust, symmetrical, slightly curved at centre,

FIG. 1. *Axinyssa tethyoides*, holotype (BMNH 1902.11.16.25). A,whole specimen (scale=30mm). B,SEM of skeleton (scale=1mm). C,spicule (scale=250μm).

tapering to sharp points (Fig. 2A) (length 533-648.4-789μm, width 18-29.6-43μm).

REMARKS

The large size of spicules, undifferentiated axial and extra-axial skeletons, lack of a condensed axial skeleton, absence of spongin fibres, presence of heavy collagen in the mesohyl, and a spherical fistulose growth form distinguish this species from all the Australian '*Pseudaxinyssa*' species. For reasons discussed above we consider that this distinction is at the generic level.

Cymbastela gen.nov.

Pseudaxinyssa, in part, Bergquist & Tizard, 1967: 190; Lévi, 1983:719.

TYPE SPECIES

Pseudaxinyssa stipitata Bergquist & Tizard, 1967:189 (holotype AM Z3101).

DIAGNOSIS

Typically stalked, cup-shaped, thinly lamellate growth form. Ectosome with or without

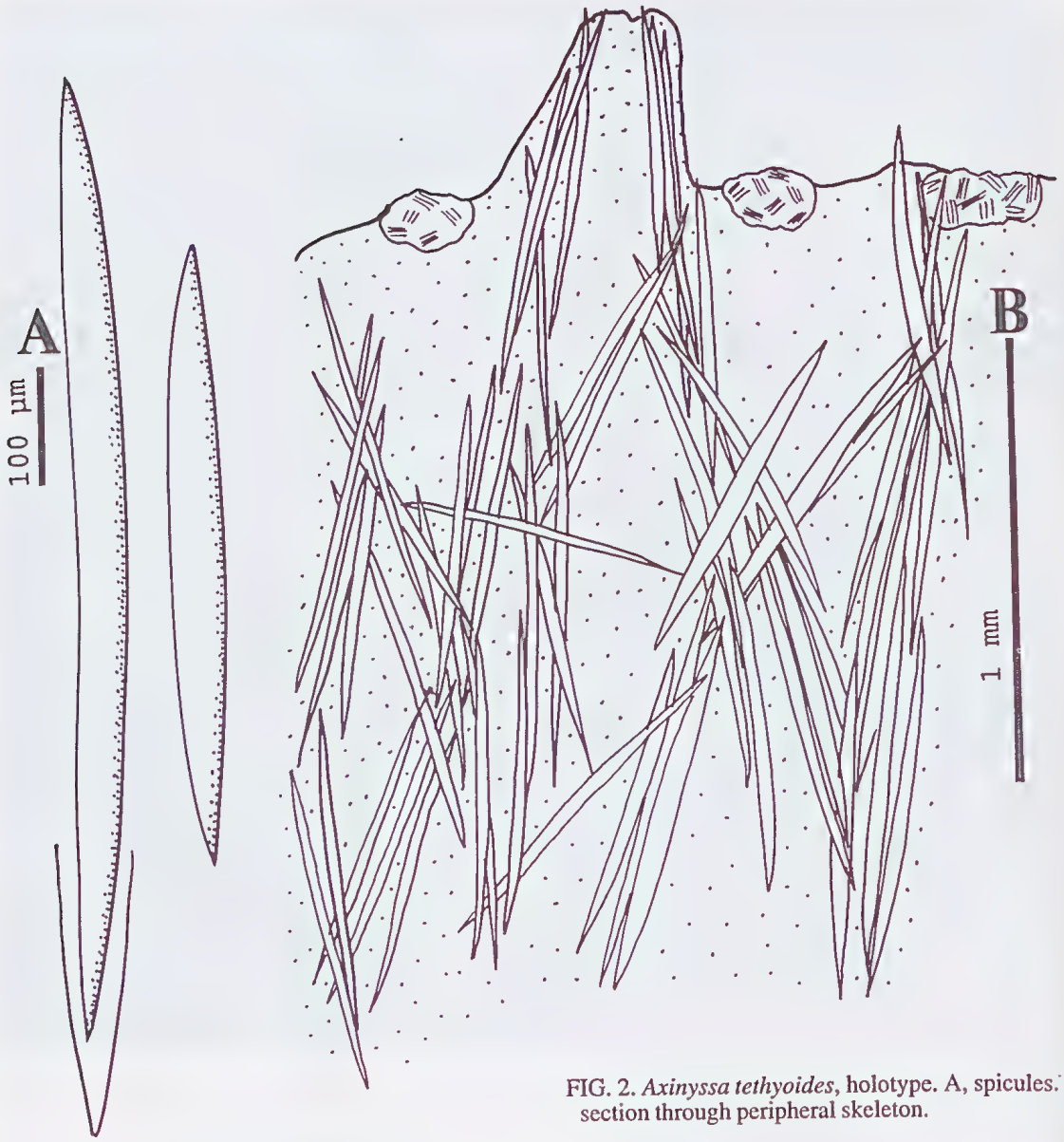


FIG. 2. *Axinyssa tethyoides*, holotype. A, spicules. B, section through peripheral skeleton.

specialised skeleton of smaller oxeas. Choanosomal skeleton with compressed reticulate axial region, in which major tracts run longitudinally through lamellae, and with gradually ascending, diverging, radial, plumose or plumoreticulate extra-axial region, in which tracts become plumose and project through surface. Spongin fibres well developed, cored by oxeas, frequently with telescoped points. Predominantly autotrophic, most species containing symbiotic cyanobacteria. Oviparous.

ETYMOLOGY

Latin, *cymba* - cup, *stela* - column (f.); *Cymbastela*, for the predominantly stalked, cup-shape growth forms.

REMARKS

Cymbastela is an unusual axinellid in its growth form, although this morphology is also repeated in several Haplosclerida, such as some *Haliclona* and *Amphimedon*. Typically the genus has a reticulated, compressed axial skeleton and a plumose extra-axial skeleton, both composed of

TABLE 1. Comparison in spicule dimensions between described species of *Cymbastela*. All measurements given in micrometres, and expressed as minimum - mean - maximum range of measurement. N=number of specimens examined.

SPECIES	OXEAS	
	Length	Width
C. cantharella (N=3)		
Holotype	187-215.5-232	4.0-8.1-10
Other specimens	143-220.1-245	2.5-8.7-12
C. concentrica (N=5)		
Type material	172-239.6-305	2.5-9.5-16
Other specimens	79-152.6-189	1.6-5.9-11
C. coralliophila (N=8)		
Holotype I	263-318.8-357	6.5-14.4-21.7
II	135-166.8-255	1.1-3.2-5.6
Other specimens I	190-293.1-356	6.1-12.5-18.6
II	119-162.5-279	1.1-3.2-7.2
C. marshae (N=3)		
Holotype	124-156.8-192	2.0-5.4-9.0
Other specimens	119-150.7-180	1.6-6.4-11.3
C. notiaina (N=1)		
Holotype	49-77.1-98	1.5-3.2-4.5
C. stipitata (N=38)		
Holotype	155-259.1-344	2.7-8.6-16.0
Other specimens	133-267.4-361	2.0-11.4-19.5
C. vespertina (N=8)		
Holotype	167-252.2-270	5.2-11.9-15.0
Other specimens	152-238.8-283	3.6-10.7-16.2

well formed spongin fibres. In the extra-axial region there are always fewer paucispicular, reticulate fibres interconnecting the multispicular, radial or plumose, ascending fibres. This structure shows some similarities to the skeletons found in *Axinella* Schmidt (i.e. *A. polypoides* Schmidt, sensu Vosmaer, 1912), in which there is a condensed, reticulate axis and plumose-branching and reticulated extra-axis, and *Phakellia* Bowerbank (i.e. *P. ventilabra* Linnaeus, sensu Vosmaer, 1912), in which there is a condensed, reticulate axis, and a plumose, radial, non-branching or poorly-branching extra-axial skeleton. Both *Axinella* and *Phakellia* have spicules consisting of styles, strongyles and oxeas, in all combinations, whereas in *Cymbastela* spicules are only oxeas, usually with telescoped ends. *Cymbastela* is superficially most similar to *Phakellia* (sensu Vosmaer), due to the emphasis of the extra-axial skeleton over other structures, but it is probably most closely related to *Axinella* in all other features.

It is difficult to define any particular character which may serve as a synapomorphy for *Cymbastela*, clearly differentiating it from its sister group *Axinella*, in particular. Virtually no single feature is unique; levels of homoplasy are comparatively high within the Axinellidae. The lamellate growth form is characteristic and consistent, but not unique to *Cymbastela*: two species of *Axinella*, *A. vaceletia* (Pansini) and *A. shoemakeri* de Laubenfels, are also lamellate. Similarly, *Axinella polycapella* de Laubenfels has a reduced spicule complement, with mostly only oxea megascleres, although in *Cymbastela* many of the oxeas have telescoped ends, and it is probably this feature that is most important in defining the genus. Therefore, all three characters in combination - growth form, spiculation and skeletal architecture - are considered to be valid discriminatory characters defining the new genus.

Seven species are referred here to *Cymbastela*, only three of which have been previously described. The genus is most common in the tropical Australian - western Pacific region, although one temperate species is also known.

KEY TO THE SPECIES OF *CYMBASTELA*

Characters found in both preserved material [and live specimens] are indicated.

1. Oxeas mostly with telescoped ends ..... 3.

   Oxeas mostly with tapering ends ..... 2.

2. Thicker lamellate, cup-shaped growth form, often with external buttresses, concentric lamellae, and lateral projections [typically pigmented olive-green and mauve]) ..... *C. stipitata* (Bergquist & Tizard).

   Thinly lamellate, usually simple, concentric or asymmetrical cup-shaped growth forms, without exterior projections [dark maroon-brown, evenly pigmented] .... *C. vespertina* sp.nov.

3. Oxeas well silicified ..... 4.

   Oxeas poorly silicified, vestigial, thin, with strongyloid-rounded telescoped ends [small symmetrical vase-shaped, thin lamellae, even surface, live colouration unknown] .....*C. notiaina* sp.nov.

4. Specialised ectosomal skeleton of smaller oxeas present, overlaying projecting subdermal skeleton of larger oxeas [wide cups or thickly lamellate lobes attached directly to substrate, usually with convoluted external surface, mot-

tled olive-green and olive-brown colouration] ..... *C. coralliophila* sp.nov.

Without specialised ectosomal skeleton ..... 5.

5. Axial skeleton not compressed, predominantly plumo-reticulate, extra-axial skeleton radial, not plumose, ectosomal skeleton with plumose projecting spicules [concentric cups, usually buttressed or with other sorts of external projections, thin lamellae, convoluted margins, with obvious differences between interior (porous, inhalant) and exterior (smooth, exhalant) surfaces, pale orange] ..... *C. cantharella* (Lévi).

Axial skeleton compressed, predominantly reticulate, extra-axial skeleton predominantly reticulate, ectosomal skeleton with plumose projecting spicules [concentric or convoluted cups, thin lamellae, evenly pigmented dark brown or olive-brown] ..... *C. concentrica* (Lendenfeld).

Axial skeleton compressed, predominantly plumose or longitudinal, less obviously reticulate, extra-axial skeleton predominantly plumose, ectosomal skeleton plumose [irregular cups, thin lamellae, no basal stalk, smooth surface on both interior and exterior faces, evenly pigmented olive-green/maroon] ..... *C. marshae* sp.nov.

Cymbastela stipitata (Bergquist and Tizard) (Figs 3-5, Table 1)

Pseudaxinyssa stipitata Bergquist and Tizard, 1967:189-191, text-figs 3-4, pl.5, fig.3.

MATERIAL EXAMINED

HOLOTYPE: AM Z3101: East Point Reef, Darwin, NT, 12°25.0'S, 130°49.1'E, intertidal, 13.x.1965, coll. E. Pope and R.S. Williams.

OTHER MATERIAL: (All material collected by the author unless otherwise indicated). DARWIN REGION, NT: NTM Z163-165: East Point Aquatic Life Reserve, 12°25.0'S, 130°49.1'E, 0.5m depth, 13.xi.1981 (stn EP6). NTM Z261 (4 specimens): same locality, 17.ix.1981 (stn EP3). NTM Z294: same locality, 1m depth, 18.viii.1981 (stn EP4). NTM Z309: same locality, 0.5m depth, 20.ix.1981 (stn EP5). NTM Z2145: same locality, 27.ix.1984 (stn EP17). NTM Z2207: same locality, 23.xi.1984 (stn EP18). NTM Z2225: same locality, 22.i.1985 (stn EP20). NTM Z2240: same locality, 8.iii.1985 (stn EP21). NTM Z2250: same locality, 12.iv.1985 (stn EP22). NTM Z2412: same locality, 7.x.1975 (stn Don.196, coll. A.J. Dartnall). NTM Z2422: same locality, 3m depth, 14.viii.1985 (stn EP24). NTM Z2542: same locality, 0.5m depth, 4.x.1985 (stn EP25). NTM Z2547: same locality, 15.xi.1985 (stn EP26; coll. A.M. Mussig). NTM Z2552: same locality, 12.xii.1985 (stn EP27; coll. A.M. Mussig and C. Hood). NTM Z2250: same locality, 12°24.5'S, 130°48.0'E, 10m depth, 12.iv.1985, coll. C. Hood and J.R. Hanley (stn EP22). QM G300001 (fragment NTM Z2392): same locality, 8m depth, 29.vii.1985 (stn EP23). NTM Z3179: same locality, 12°29.5'S, 130°48.0'E, 0.5m depth, 10.ix.1987, coll. N. Smit, by hand (stn JH-87-017). NTM Z401: Vestey's Beach, 12°26.2'S, 130°49.9'E, intertidal, 11.xii.1981 (stn MB4). NTM Z479: Fannie Bay beach, 12°25.0'S, 130°50.0'E, intertidal, 9.ii.1982 (stn EP7). NTM Z2009

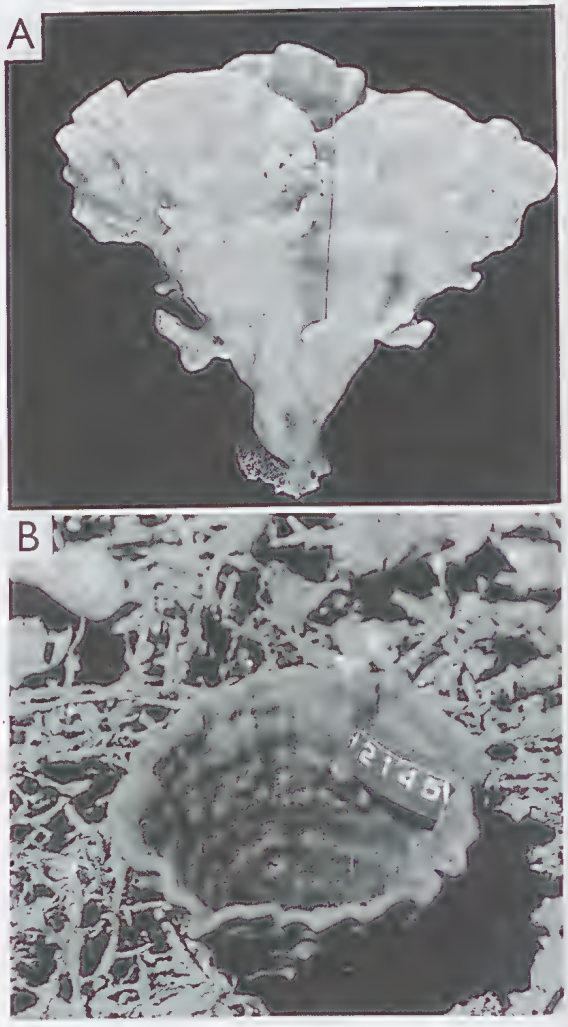


FIG. 3. *Cymbastela stipitata*. A, typical growth form (specimen NTM Z2009). B, in situ (specimen NTM Z2145).

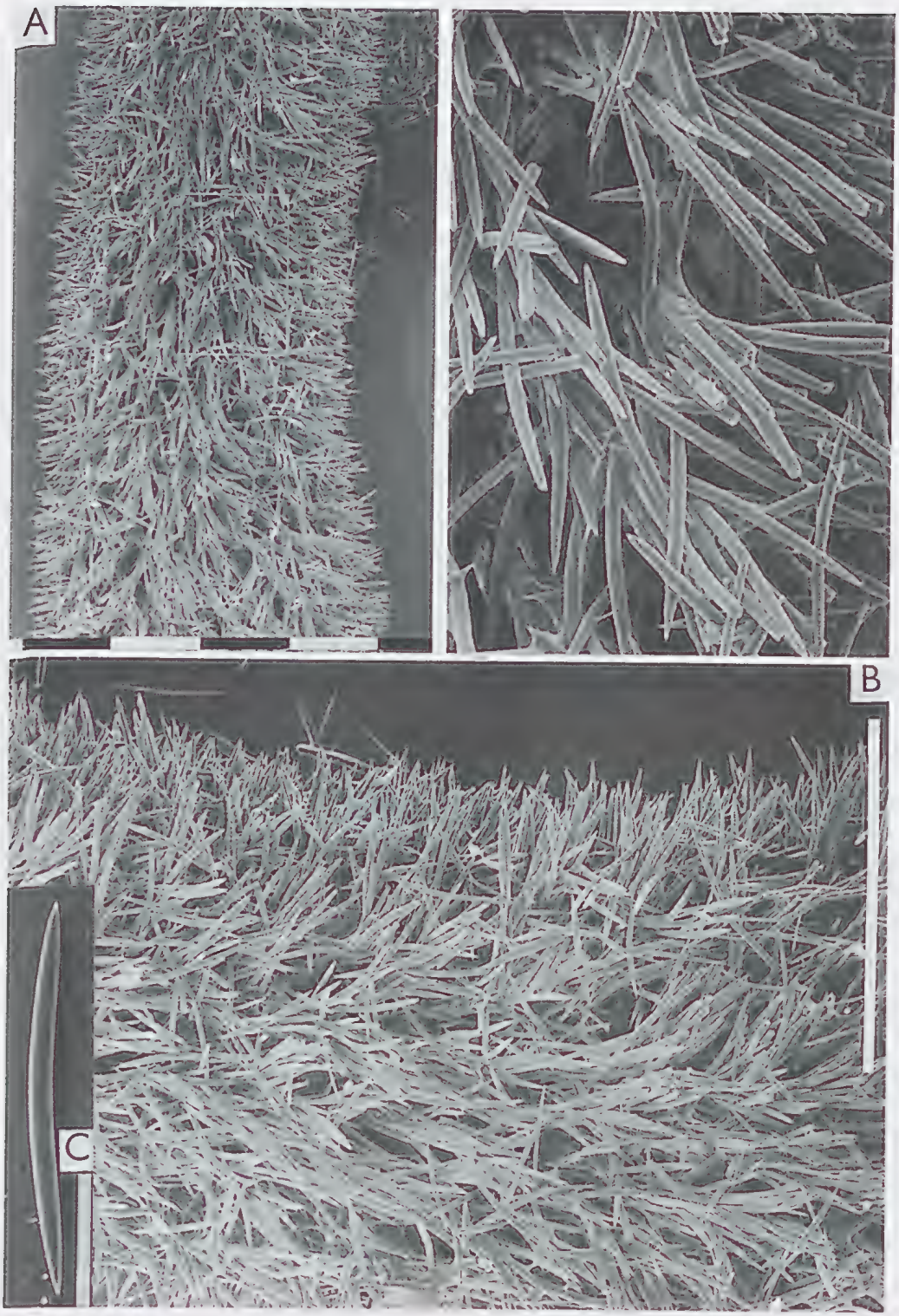


FIG. 4. *Cymbastela stipitata*. A, SEM of skeleton (specimen NTM Z2009) (scale=500μm; left magnified 40.8 times, right magnified 320 times). B, peripheral skeletal architecture (scale=1mm). C, oxea (scale=100μm).

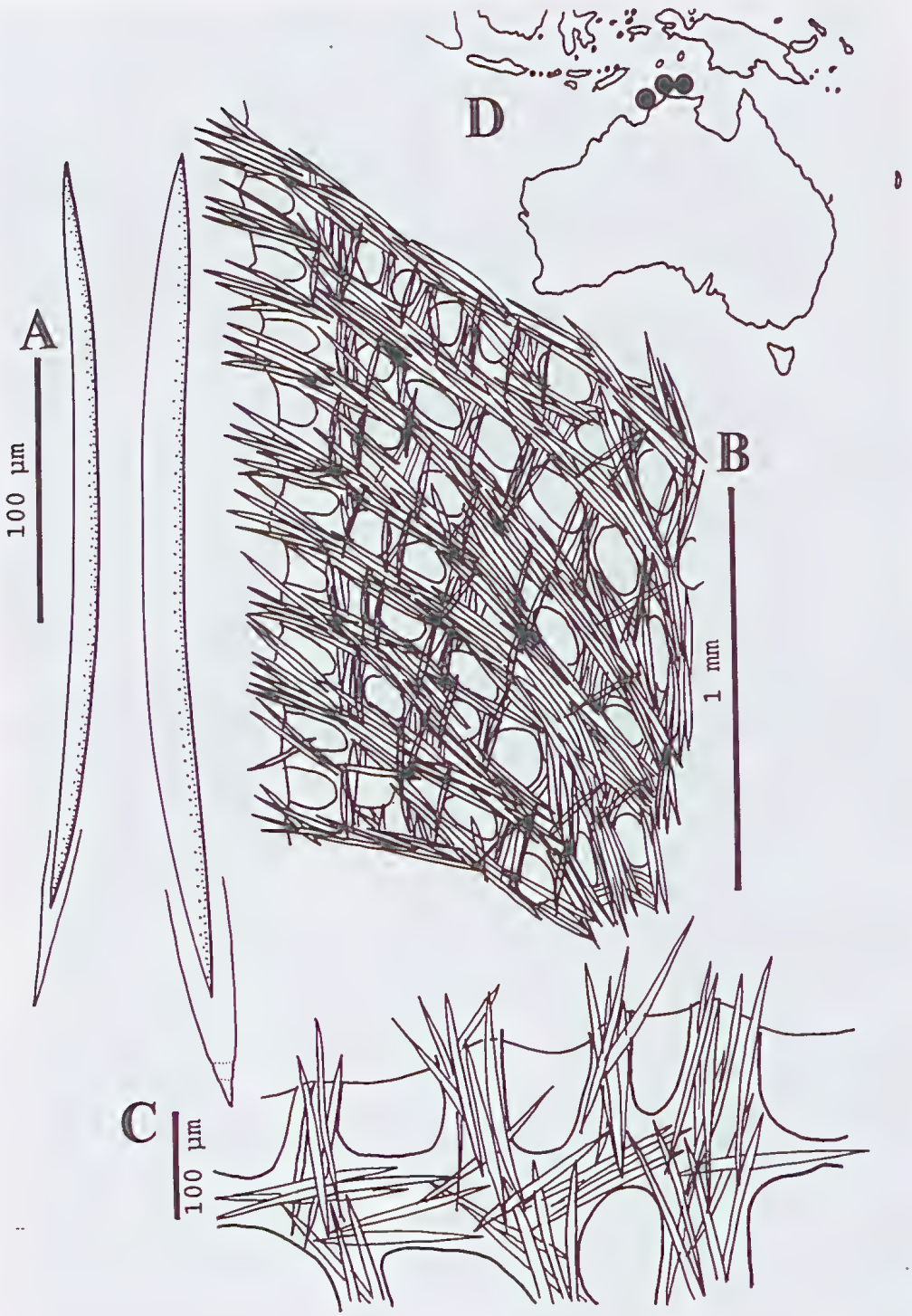


FIG. 5. *Cymbastela stipitata*, specimen NTM Z2009. A, spicules. B, section through peripheral skeleton. C, enlarged portion showing the close-meshed reticulate near the axial skeleton. D, confirmed distribution.

(fragment QM G300006): W side of Weed Reef, 12°29.2'S, 130°47.1'E, 19m depth, 11.v.1984 (stn WR2). NTM Z2190: 'Bommies', Weed Reef, 12°29.2'S, 130°37.6'E, 6-10m depth, 16.xi.1984 (stn WR6). SAM TS4023 (fragment NTM Z1655): Old Man Rock, Nightcliff, 12°21'S, 130°51'E, intertidal, 16.vi.1962 (coll. R.N. Southcott and A.E. Adams, stn A573). NTM Z424: Lee Point, 12°19.2'S, 130°53.1'E, intertidal, 13.xii.1981 (stn LP2). NTM Z779: W side of Channel I., Middle Arm, 12°33.4'S, 130°52.5'E, 2m depth, 7.vii.1982 (stn CI2). NTM Z796: S side of Channel I., Middle Arm, 12°32.3'S, 130°51.3'E, 11m depth, 16.vii.1982, coll. S. Chidgey. NTM Z2105: N side of Fish Reef, Bynoe Harbour 12°26.2'S, 130°26.2'E, 9-10m, 5.ix.1984 (stn FR2). Cobourg Peninsula Region, NT - NTM Z2491: Coral Bay (now known as Seven Spirit Bay), Port Essington, 11°09.4'S, 132°04'E, 4-7m depth, 13.ix.1986 (stn CP71). NTM Z3301, 3302: Inside outer barrier to Coral Bay, S side of Bay, Port Essington, 11°09.4'S, 132°04.0'E, 2-7m depth, 12.ix.1986, SCUBA (stn JH-85-020). NTM Z3244: SW side of cliff face, Table Head, Port Essington, 11°13.5'S, 132°10.5'E, 2-5m depth, 11.ix.1986, SCUBA (stn JH-85-019). NTM Z119: Sandy I. No. 2, Arafura Sea, 11°05.5'S, 132°17'E, 7m depth, 20.x.1981 (stn CP26). NTM Z536: E of Point Edwards, Port Bremer, CPMNP, 11°08.5'S, 132°18.8'E, 6-7m depth, 1.v.1982 (stn CP33).

Substrate and Depth Range

Restricted to shallow coastal waters, ranging from intertidal to 19m depth. Substrate predominantly rock or coral rubble, and the sponge is most abundant in areas where there are relatively light loads of sediment.

Geographical Distribution

Northwestern Australian waters (Fig. 5D). Lévi (1983) suggested that *C. stipitata* also occurs in the lagoon off Noumea, New Caledonia, but it is possible that he was referring to the new species described below from the Great Barrier Reef, *Cymbastela coralliophila* sp.nov.

Description

Shape: Stalked, cup-shaped growth form, usually with thick, uneven, crenellated margins, smooth interior surface, mostly smooth exterior surface of vase, but often with lateral growths and projections on exterior surface. Growth variants common, sometimes with 2-4 concentric, successively smaller cups growing inside each other, with or without buttressed exterior projections near base. Margins and stalk typically relatively thick, up to 14mm and 32mm maximum widths, respectively. Although growth variants may occur within metres of each other, specimens tend to be thinner, more elongate (more vasiform), and less convoluted with increasing depth (Figs 3A,B).

Surface features: Oscules not visible optically, although small, evenly distributed pores (0.8-1.8mm diameter) seen under higher magnification, usually situated on points of surface conules. In some cases distribution of pores coincides with distribution of parasitic barnacles (*Acasta* sp.), whereas other openings appear to be true inhalant or exhalant pores.

Colour: Live colouration clearly dependent on well-being of resident algal symbionts - variations in pigmentation related to degree of shading, water depth and water clarity. Typical live colouration of intertidal specimens olive-green on margins (Munsell 2.5GY 5/4), olive-green with maroon-brown tinge on inside of vase (5GY 4/4-2.5R 4/2), maroon-brown on exterior of vase and stalk (2.5R 4/4). Subtidal specimens typically evenly pigmented olive-brown or olive-maroon (2.5-10R 3/2). Heavily shaded, damaged specimens or material from waters with exceptionally high turbidity may be completely beige (i.e. without pigments).

Texture: Consistency always stiff, firm, but flexible, with roughened, sand-paper texture produced by spicules protruding slightly from dermal skeleton. Surface always optically smooth, microscopically hispid and microconulose, frequently raised into regular or irregular ridges or rounded digitate projections.

Ectosome: No specialized skeleton on surface, but with prominent, relatively closely meshed, diverging plumose brushes of choanosomal oxeas protruding through ectosome for short distances (up to 150μm maximum), producing microscopic surface conules. Subdermal skeleton more-or-less plumose, with more closely meshed multispicular skeletal tracts than on ectosome. Tracts may or may not be interconnected by paucispicular transverse fibres, but usually hidden by diverging spicules (Figs 4, 5B-C).

Choanosome: Axial skeleton compressed, composed of very close-meshed plumose or vaguely plumo-reticulate multispicular fibres, mostly running longitudinally along core of lamellae, occupying majority of lamella diameter. Only few interconnecting uni- or paucispicular tracts observed at core, but these mostly obscured by close-meshed reticulation. Disjunction between longitudinally orientated axial skeleton and vertically disposed extra-axial skeleton only noticeable very close to periphery. Choanosomal fibres

lightly invested with spongin, with few extra-fibre megascleres. Mesohyl matrix lightly reinforced with collagen, with abundant microalgae scattered throughout.

Spicules (refer to Table 1 for dimensions): Megascleres unmodified oxeas, symmetrical, thick, curved centrally, with mostly fusiform sharply pointed ends, sometimes with very slightly telescoped points but this feature never as well developed as in other species. Structural megascleres coring fibres slightly larger than those scattered between fibres (Fig. 5A).

ASSOCIATIONS

With the exception of a few specimens from very turbid waters, which may have shed their algal symbionts, most specimens of *C. stipitata* contained cyanobacteria (blue-green algae), dispersed evenly throughout the sponge mesohyl. Only rarely were these symbionts seen inside spongin fibres. The olive-green, olive-brown sponge pigmentation, characteristic of this species, may be a photosynthetic by-product of these symbionts: the several shallow water specimens tested were chlorophyll positive (as demonstrated by acetone extracts of tissues). Parasitic barnacles of the genus *Acasta* are also common within this sponge.

REMARKS

This species is immediately differentiated from other tropical Australasian *Cymbastela* species by the emphasis of its plumose skeletal architecture over other skeletal components. In other species the reticulate connections within the skeleton are more obvious, and overall skeletal architecture is predominantly plumo-reticulate, but in *C. stipitata* the reticulate component of the skeleton is masked slightly by the dense plumose tracts. In this regard the species is most similar to *C. marshae* sp.nov. from the Houtman-Abrolhos Is, WA, which has much smaller spicules (Table 1). In some respects it also resembles the northwestern Australian *C. vespertina*, which is found in deeper, less turbid waters. The latter species, however, has much thinner lamellae and is usually evenly pigmented maroon-brown to purple-grey alive. *Cymbastela stipitata* is contrasted further with other species below.

Cymbastela vespertina sp.nov.
(Figs 6-8, Table 1)

Pseudaxinyssa n.sp.; Hooper et al., 1992: Table 1, Fig 3b.

MATERIAL EXAMINED

HOLOTYPE: NTM Z3939 (fragment QM G300010): N side of Cumberland Strait, Wessel Is, NT, 11°27.6'S, 136°28.7'E, 32m depth, 15.xi.1990, coll. J.N.A. Hooper, SCUBA (stn JH-90-028). PARATYPES: NTM Z2615: East Point Aquatic Life Reserve, Darwin, NT, 12°24.5'S, 130°48.0'E, 9-12m depth, 3.iv.1986, coll. J.N.A. Hooper, SCUBA (stn EP28). QM G300002 (fragment NTM Z3948): S of W headland, Rimbija I., Cape Wessel, Wessel Is, NT, 11°0.5'S, 136°43.8'E, 15m depth, 16.xi.1990, coll. J.N.A. Hooper, SCUBA (stn JH-90-030).

OTHER MATERIAL: (All material collected by the author unless otherwise indicated). NORTHWEST SHELF REGION, WA: NCI Q66C-1323-F (fragment NTM Z3470): Offshore from Norcape Lodge, Learmonth, Exmouth Gulf 21°56.6'S, 114°09.1'E, 6m depth, 17.viii.1988, coll. NCI, SCUBA. DARWIN REGION, NT: NTM Z2696: East Point Aquatic Life Reserve, 12°24.5'S, 130°48.0'E, 9-12m depth, 3.iv.1986, coll. J.N.A. Hooper, SCUBA (stn EP28). NTM Z2699: East Point Aquatic Life Reserve, 12°24.5'S, 130°48.0'E, 9-12m depth, 3.iv.1986 (stn EP28). ARAFURA SEA, NT: NTM Z3069, NCI-Q66-0519-F: Parry Shoals, 11°11.72'S, 129°43.26'E, 16m depth, 12.viii.1987, coll. A.M. Mussig, SCUBA (stn AM 87-2). WESSEL ISLANDS, NT: NCI Q66C-4828-O: S of W headland, Rimbija I., Cape Wessel, 11°0.5'S, 136°43.8'E, 15m depth, 16.xi.1990, coll. NCI, SCUBA (stn JH-90-030).

SUBSTRATE AND DEPTH RANGE

Patch rock reef, fringing coral reef, or rock heads, sandy bottom over hard corals, gorgonians, sponges and algae, in areas of strong current; 6-32m depth range.

GEOGRAPHICAL DISTRIBUTION

Northwest coast of Australia, from Exmouth Gulf to Wessel Islands (Fig. 8C).

ETYMOLOGY

Latin, *vespertinus*, western, or of the evening; for the west Australian coastal distribution of this species.

DESCRIPTION

Shape: Thin-walled, lamellate, cup shaped sponges, 95-190mm high, 70-170mm maximum diameter, lamellae 2-4.5mm thick. Lamellae typically do not rejoin completely, usually producing asymmetrical cups. Apical margins of lamellae usually even, but larger specimens may consist of 2-4 concentric cups, with lamellae forming spiral walls. Sponges attached to substrate by large, flat basal plates, up to 55mm maximum diameter, with

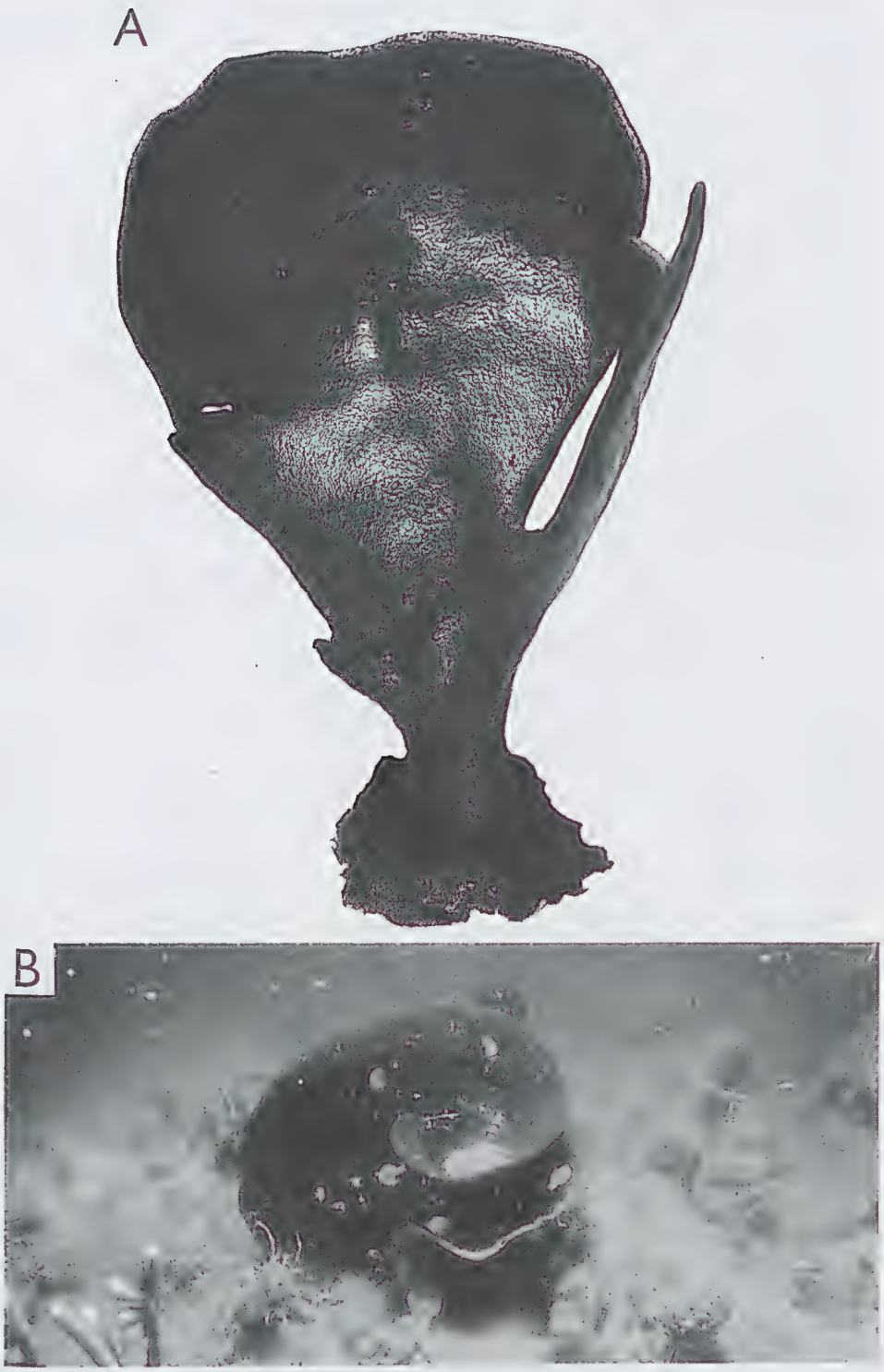
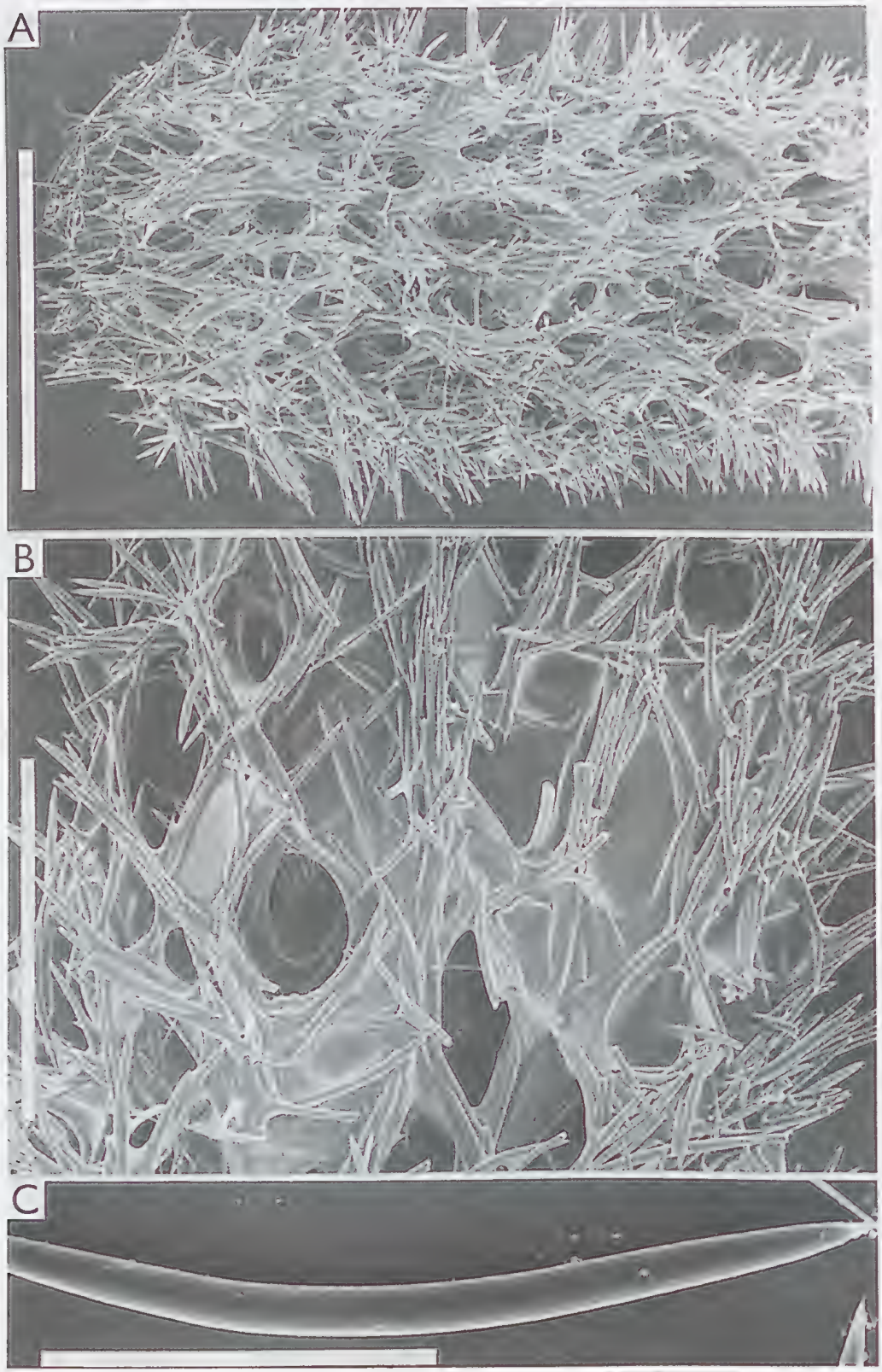


FIG. 6. *Cymbastela vespertina* sp.nov. A, holotype (NTM Z3939). B, paratype (NTM Z2615), in situ.


A
B
C

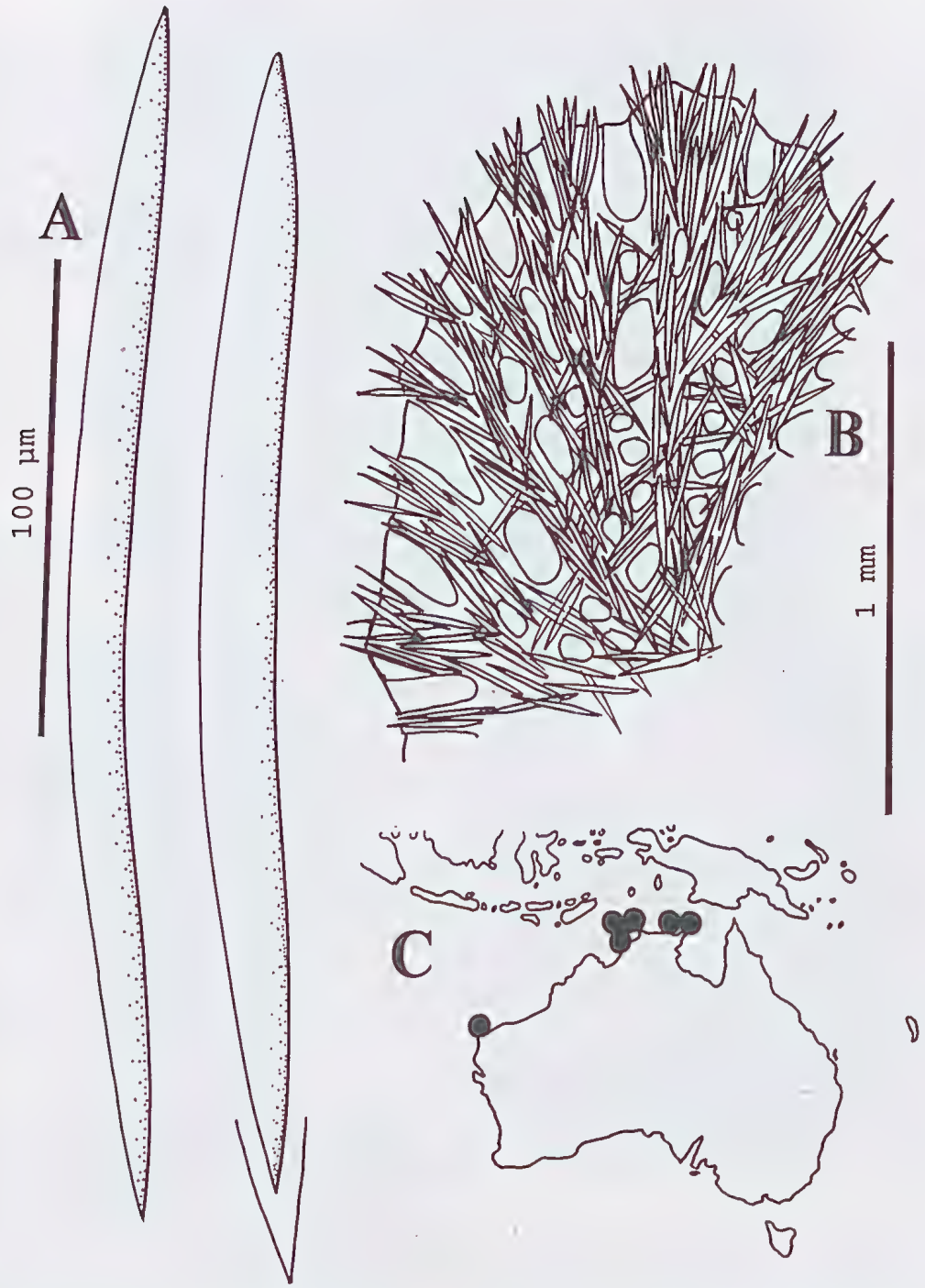


FIG. 8. *Cymbastela vespertina* sp.nov. (holotype NTM Z3939). A, spicules. B, section through peripheral skeleton. C, known distribution.

FIG. 7. *Cymbastela vespertina* sp.nov. (paratype QM G300002). SEMs of skeleton showing: A, section through lamella (scale=1mm); B, slightly compressed plumo-reticulate axial arrangement (scale=500µm); C, oxeas and terminations (scale=100µm).

short, thick stalk, 14-36mm long, 14-28mm diameter (Fig. 6A,B).

Surface features: Smooth, even, uninterrupted by any surface processes. Microscopically surface with minute conules. Oscules not seen, but small evenly distributed pores, up to 0.8mm diameter, scattered over surface of lamellae.

Colour: Live colouration dark maroon brown (Munsell 2.5R 4/4) to greyish purple (5R 5/2), always evenly pigmented, whereas in ethanol colour usually dark brown or dark grey.

Texture: Firm, slightly compressible texture, sandpaper-like to touch.

Ectosome: Membraneous, without specialised spiculation, but with regularly spaced plumose brushes, composed of 3-8 oxeas, from ascending extra-axial tracts, protruding through surface for short distances, up to 100μm from ectosome. Position of plumose spicule brushes on surface coincides with minute surface conules. Subectosomal region predominantly plumose, slightly plumo-reticulate, with ascending plumose portion of skeletal tracts greatly emphasised over uni- or paucispicular reticulate, transverse, connecting tracts. Spongin fibre mesh size in peripheral skeleton up to 140μm diameter, more open than in axial region (Figs 6,7).

Choanosome: Skeleton slightly axially compressed, plumo-reticulate, with plumose component emphasized only slightly over reticulate component of skeleton: former consisting of multispicular ascending tracts, latter with paucispicular, connecting tracts, both enclosed within spongin fibres (Fig. 8B). Spongin fibres light but well developed, with small mesh sizes, up to 90μm maximum diameter. Mesohyl with moderate quantities of brown-pigmented collagenous spongin, and only few spicules dispersed outside fibres. Choanocyte chambers oval, 28-90μm diameter.

Spicules (refer to Table 1 for dimensions): Megascleres oxeas without any modifications, relatively long, slender, slightly curved centrally, tapering to sharp fusiform points, with very few examples bearing telescoped points (Fig. 8A).

Associations

This species is usually associated with symbiotic microalgae (cyanobacteria) in shallow water (i.e. is chlorophyll positive), and the symbionts are probably responsible for producing the characteristic dark purple-mauve live pigmentation, although one specimen (Z3939) was pale beige in situ and may have shed its algae. Parasitic barnacles are rare.

Remarks

This species was originally thought to be merely a modified, deeper-water form of *C. stipitata*, as there are similarities in skeletal architecture and spicule dimensions. However, morphological differences described above, particularly the asymmetrical cup shape, the very thin lamellae and darker pigmentation, and differences in free amino acid profiles between *C. vespertina* and *C. stipitata* (Hooper et al., 1992), indicate that these two sympatric populations are heterogenous and sibling species.

Cymbastela concentrica (Lendenfeld) comb.nov. (Figs 9-11, Table 1)

Antherochalina concentrica Lendenfeld, 1887:788, pl.22, fig.42.

Material Examined

Lectotype (here designated): AM Z1993: Port Molle (now Airlee Beach), Qld, 20°13'S, 148°49'E, no other collection details known. (cf. published locality of St Vincent Gulf, South Australia). Paralectotypes: BMNH 1886.8.27.451, 460: same locality.

Other Material. Queensland - NTM Z3169 (fragment QM G300009): Outer slope of reef front, Blue Lagoon, Lizard I., Great Barrier Reef, 14°40'S, 145°48'E, 10-20m depth, 1987, coll. A.W.D. Larkum (ref.no. PC 348T, PC 346). QM G300003: Inner Gneerings, Moreton Island, 26°38.5'S, 153°09.5'E, 14m depth, 01.v.1991, coll. Thorogood, JA, SCUBA (ref.JT-8).

Substrate and Depth Range

Inshore fringing reefs and coral reef slope, up to 20m depth.

Geographical Distribution

Northern, central and southern Queensland (Fig. 11C).

Description

Shape: Cup- or vase-shaped growth forms, up to 150mm high, 125mm maximum width, consisting of relatively thin (approximately 2mm wide), convoluted, conical lamellae or symmetrical cups on short basal stalk. Stalk length up to 45mm long, 25mm diameter. Lamellae may produce concentric whorls inside cup, or merely contain a few irregular bumps; margins of lamellae slightly convoluted (Fig. 9A-C).

Surface features: Lamellae smooth, slightly irregular, with low conules and ridges on exterior surface, more even interior surface; no buttresses or external processes.

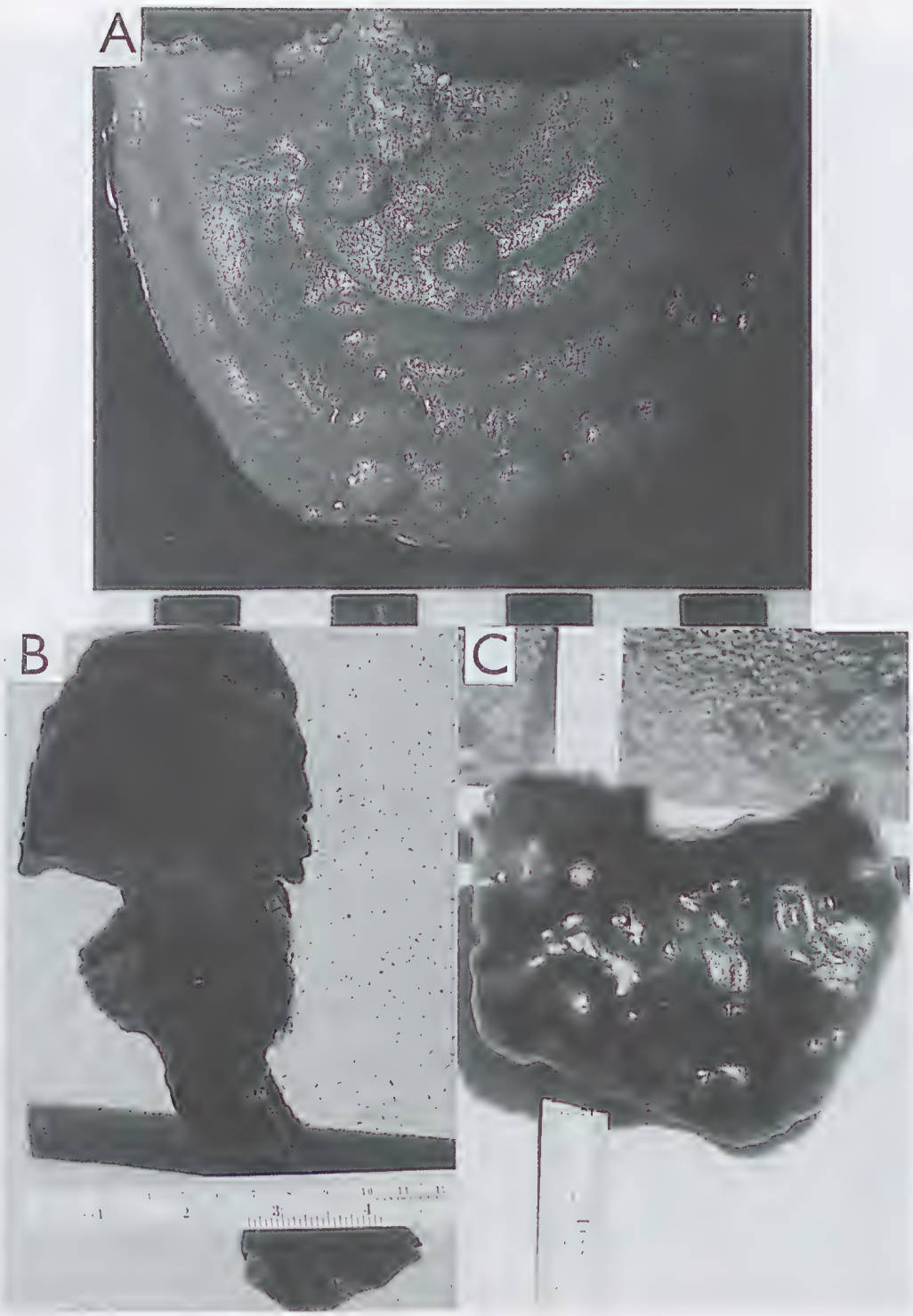


FIG. 9. *Cymbastela concentrica*. A, Paralectotype (BMNH 1886.8.27.451). B, specimen (NTM Z3169; photo A. Larkum). C, field number PC 346, unaccompanied by voucher specimen (photo A. Larkum).

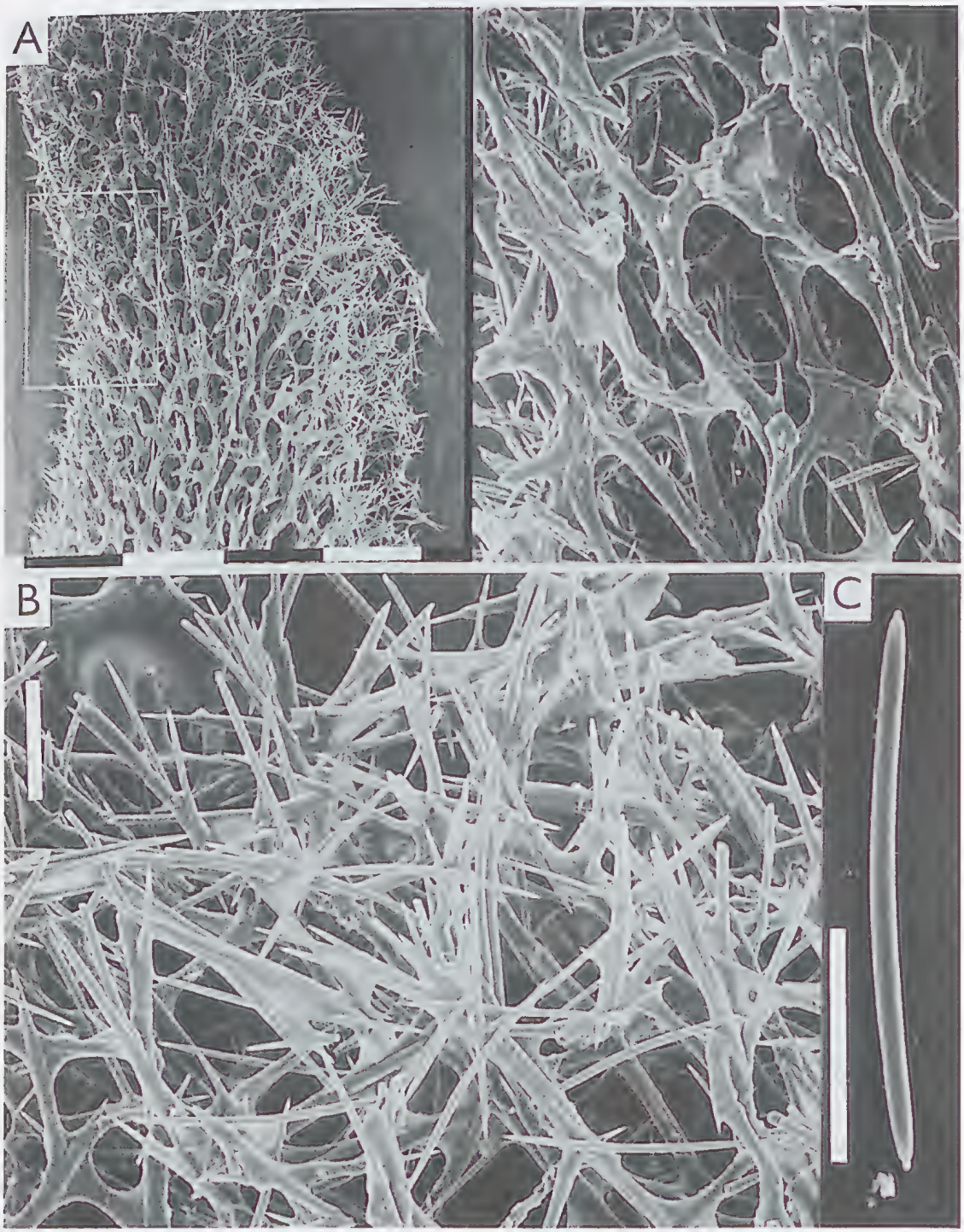


FIG. 10. *Cymbastela concentrica*. A, SEM of skeleton (specimen NTM Z3169) (scale=500μm; left magnified 21.2 times, right magnified 186 times). B, peripheral skeletal architecture (scale=100μm). C, spicule with telescoped ends (lectotype AM Z1993) (scale=50μm).

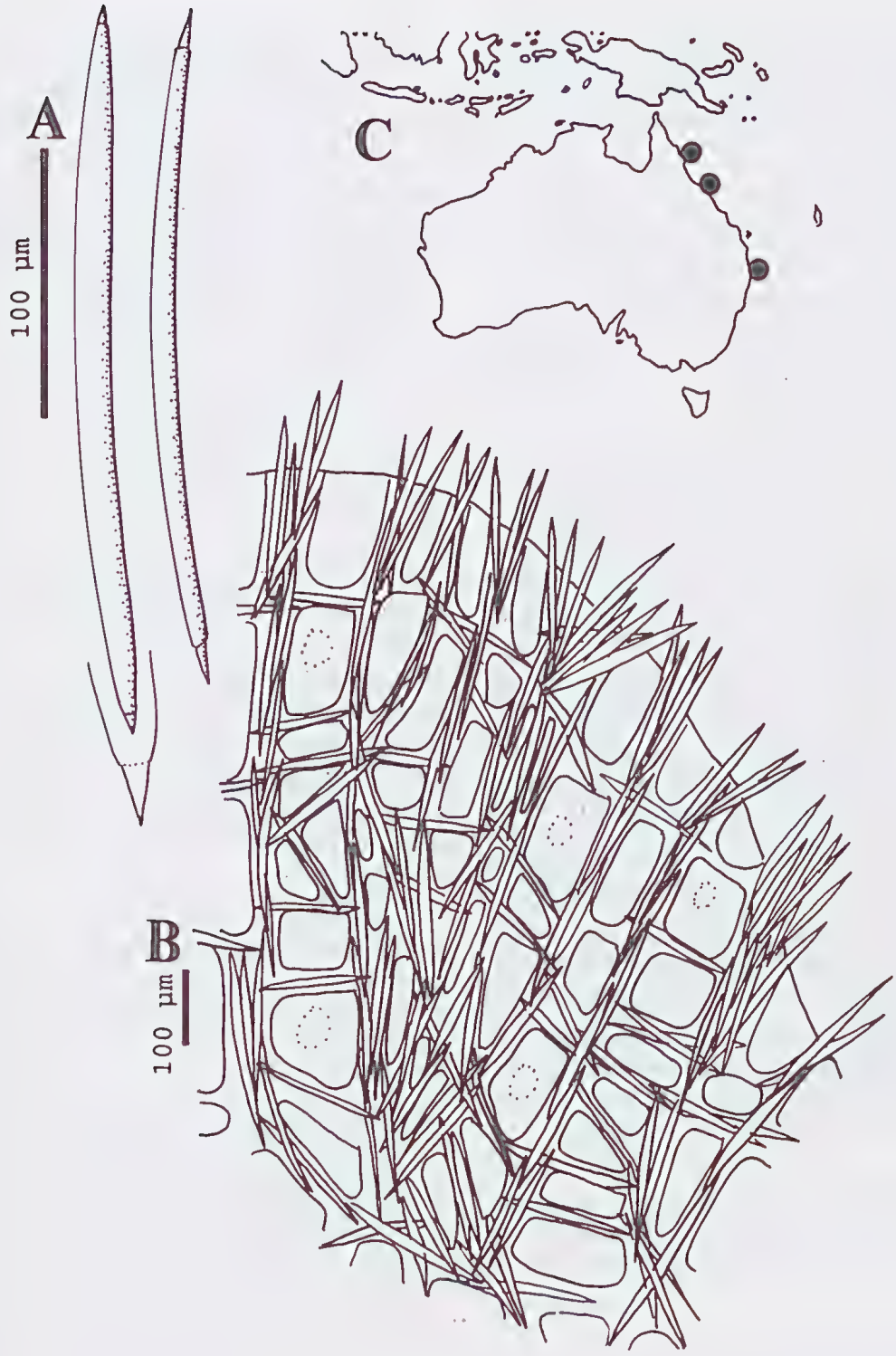


FIG. 11. *Cymbastela concentrica*, lectotype (AM Z1993). A, spicules. B, section through peripheral skeleton. C, known distribution.

Colour: In life, dark brown (interior) (Munsell 5YR 3/2) or olive brown (exterior) (2.5YR 4/4). Chlorophyll pigments abundant (seen in acetone extracts of freshly preserved material), due to presence of large population of cyanobacteria (microalgal) symbionts.

Texture: Smooth, stiff and flexible consistency, with a slightly velvet surface texture.

Ectosome: Optically smooth, lacking specialized skeleton, but microscopically villose, with substantial portions of spicule from peripheral skeleton protruding through surface and forming plumose brushes. Spicules protrude up to 230μm from surface, and brushes may contain up to 8 spicules (Figs 10, 11B). Microalgae, seen in fresh material, appear to be concentrated near periphery of skeleton.

Choanosome: Skeletal architecture plumo-reticulate, with poorly differentiated axial and extra-axial skeletal regions - reticulate skeleton emphasised over plumose portion (Figs 10, 11B). Central region of choanosomal skeleton only slightly axially condensed, predominantly reticulate, with plumose paucispicular ascending tracts curving gradually towards surface, interconnected by uni- or paucispicular transverse tracts, whereas peripheral skeleton more clearly diverges into plumose ascending multi- or paucispicular tracts, interconnected by uni- or paucispicular transverse tracts. Spongin fibres and spicule tracts, 40-60μm wide in axis, become less heavily cored and more widely spaced towards periphery, 20-40μm wide, ultimately forming distinctive plumose dermal brushes. Spongin fibres (22-60μm wide) lightly developed, nearly fully cored by megascleres, producing ovoid to eliptical meshes (42-77μm, 60-185μm wide in axial and extra-axial regions respectively). Collagen abundant in mesohyl but very lightly pigmented. Choanocyte chambers oval to elliptical, 45-150μm diameter.

Spicules (refer to Table 1 for dimensions): Variable length, relatively, slender, fusiform oxeas, moderately curved at centre, usually with very faintly telescoped points (Fig. 11A).

Associations

Cyanobacteria were only seen in freshly preserved material, not in the type material, and appears to be concentrated mainly in the peripheral skeleton.

Remarks

Lendenfeld (1887) states that *C. concentrica* was originally collected from St Vincent Gulf, South Australia, whereas both the AM and BMNH registers, and the specimen labels with the type material, indicate that the collection locality was Port Molle, Queensland. Although the exact type locality of this species will always be doubtful, the new record of the Queensland material described here from Lizard and Moreton Is suggests that the Museum register notations may be correct. According to Burton (1934:558), and notes in the BMNH register (in M. Burton's handwriting), this species has some similarities with *Phakellia flabellata* (Carter) from southern Australia. However, the skeletal architecture and spiculation of *C. concentrica* is quite different from that of *Phakellia*, and the two species are regarded as convergent in these two superficially prominent features.

The redescription presented above differs slightly from the description given by Lendenfeld (1887), who recorded oxea dimensions of 130x5μm. In this regard his description conforms more closely to the new specimens described above than to the type material (Table 1). Apart from their smaller spicule dimensions these two specimens are identical to the type material in growth form, including lamellae thickness and surface features, skeletal architecture, spicule-spongin fibre structure and spicule geometry, and it is suggested here that all five specimens of *C. concentrica* described above are conspecific. However, the existence of these two anomalous specimens casts some doubt over the accuracy of absolute spicule dimensions as a useful diagnostic character within this genus (see Fig. 24), suggesting that spicule size may vary with latitudinal distribution.

Cymbastela concentrica is similar to most of the other lamellate Australasian *Cymbastela* species in a number of features. Many species contain symbiotic algae (i.e. are chlorophyll positive), they all have a thin, lamellar, plate-like, cup- or vase-shaped growth form, with well developed spongin fibres, and a more-or-less slightly condensed plumo-reticulate axial skeleton, plumose or plumo-reticulate extra-axial skeleton, and if present, a plumose ectosomal skeleton. Species appear to differ substantially only in spicule dimensions, spicule geometry (presence or absence of telescoped points, and possession of hastate or fusiform points), and the degree to which the skeleton is organized into axial and extra-axial sections. For example, *C. stipitata* (from inshore waters of northern Australia) has larger megascleres, spicules are only rarely terminated by telescoped points, and there is a more obvious differentiation between the axial and extra-axial regions of the skeleton, including a more con-

densed axial core, and an emphasis on the plumose portion of the skeleton. *Cymbastela cantharella* from the outer reefs of New Caledonia also has a stalked lamellar growth form, slightly differentiated axial and extra-axial skeletons, but it has distinctive orange, yellow-orange live colouration, and relatively slender oxeas. In contrast, *Cymbastela concentrica* has a relatively poorly differentiated axial and extra-axial skeleton, only slightly condensed choanosomal axis with emphasis on the reticulate extra-axial portion of the skeleton. This takes the form of a plumo-reticulate extra-axial skeleton, a plumose ectosome, and oxeas which are similar in size to those of *C. cantharella.*

Cymbastela cantharella (Lévi)
(Figs 12-14, Table 1)

Pseudaxinyssa cantharella Lévi, 1983:719-722, fig.1, pl.1.

MATERIAL EXAMINED

HOLOTYPE: MNHN LBIM DCL3141: Outer reef, SW coast New Caledonia, 40m depth, no other details known.

OTHER MATERIAL: NTM Z3869: Precise locality unknown, Noumea lagoon, SW coast, New Caledonia, 22°20'S, 166°13'E, 25m depth, coll. ORSTOM, SCUBA (ref. R1261). NTM Z3872 (fragment QM G300004): Exterior of Grand Recif Mbere, off Noumea, New Caledonia, 22°20'S, 166°13'E, 30m depth, 21.ix.1990, coll. J.N.A. Hooper, SCUBA (stn JH-90-018).

SUBSTRATE AND DEPTH RANGE

Slope and ledges near base of barrier reef, dead coral and silt substrates, 15- 75m depth.

GEOGRAPHICAL DISTRIBUTION

Known only from the New Caledonia region (Fig. 14C).

DESCRIPTION

Shape: Short, erect cup-shaped or semi-vasiform lamellae, 80-150mm high, up to 170mm maximum diameter, on short stalk, 30-40mm long, 10-17mm diameter, with thin lamellate walls, 3-6mm diameter, usually with convoluted margins, occasionally with secondary cups or lamellae growing inside primary cup, often with buttresses and secondary projections (Fig. 12A).

Surface features: Surface of lamellae predominantly smooth, although distinct differences between interior (inhalant) and exterior faces of cups exist. Exterior of lamellae microscopically smooth, optically uneven, interior of cup with numerous small oscules, 0.5-2mm diameter, each surrounded by slightly raised membraneous lip (Fig. 12B). Oscules approximately 2mm apart, throughout interior surface of lamellae producing concentric striations within interior of cup.

Colour: Pale orange alive (Munsell 2.5-7.5 YR 8/10), beige in ethanol.

Texture: Firm, flexible, slightly compressible; exterior of lamellae with sandpaper like texture, interior more compressible.

Ectosome: Membraneous, without specialised skeleton, with heavy layer of slightly darker collagen, up to 80μm wide, through which choanosomal oxeas protrude for about half their length. Projecting oxeas occur individually or in paucispicular plumose bundles, regularly dispersed across surface, arising from ascending radial tracts in peripheral skeleton (Figs 13, 14B).

Choanosome: Choanosomal skeleton plumo-reticulate, without axial compression or any noticeable differentiation between axial and extra-axial regions, apart from plumose ectosomal spicules (Fig. 14B). Two components of skeleton predominant: first, radial spongin fibres, cored by multispicular tracts of oxeas, run longitudinally through lamellae, and gradually ascend to surface, becoming plumose and diverging near periphery; second, radial fibres interconnected by uni- or paucispicular tracts of oxeas, only weakly organised as a reticulum. The skeleton in places is almost halichondroid (Fig. 13). Spongin fibres only lightly invested in spongin, up to 75μm diameter, forming elongate or rectangular meshes, up to 125μm diameter, with small oval choanocyte chambers, 25-40μm diameter. Mesohyl heavily reinforced with collagen and containing scattered small (possibly juvenile) spicules.

Spicules (refer to Table 1 for dimensions): Oxeas relatively short, slender, slightly curved at centre, occasionally asymmetrical, tapering, fusiform, sharply pointed but usually with very slightly telescoped points at absolute apex of spicule (Fig. 14A).

ASSOCIATIONS

No symbiotic cyanobacteria were seen in any of the three specimens examined.

REMARKS

Cymbastela cantharella is apparently unlike all other species of the genus in that it contains a number of biologically active metabolites (Lévi, 1983, and pers.comm.), although the nature of this

chemical activity is not yet published. It also differs from other tropical species in lacking any evidence of symbiotic microalgae, and in this respect it is similar to the two temperate species described here. *Cymbastela cantharella* has other features typical of the genus, especially growth form - being thinly flabellate with irregular, buttressed surface processes similar to those seen on *C. stipitata*, and the geometry of the oxeas is also similar in these two species. However, the New Caledonian species differs from other *Cymbastela* in external colouration (orange alive, possibly due to the lack of photosynthetic pigments found in other tropical species), prominent surface sculpturing on the oscular face of cups, skeletal architecture (having a dense radial-plumose skeleton, with a secondary paucispicular secondary reticulate skeleton, with an overall nearly-halichondroid appearance, and radial-plumose ectosomal skeleton), and specific dimensions of oxeas (Table 1).

Cymbastela coralliophila sp.nov.
(Figs 15-17, Table 1)

Pseudaxinyssa sp.; Wilkinson, 1983:411.
Pseudaxinyssa n.sp.; Bergquist et al., 1980:424, Table 1; Lévi, 1983:720.

MATERIAL EXAMINED
HOLOTYPE: NTM Z4038: S side of Blanchard Reef, Qld, 13°23.4'S, 143°44.4'E, 14m depth, 12-xii-1990, coll. J.N.A. Hooper, USSR RV 'Akademik Oparin', SCUBA (stn JH-90-054).
OTHER MATERIAL: GREAT BARRIER REEF, QLD - FAR NORTHERN SECTION: NTM Z4039: S side of Blanchard Reef, 13°23.4'S, 143°44.4'E, 14m depth, 12-xii-1990, coll. J.N.A. Hooper, USSR RV 'Akademik Oparin', SCUBA (stn JH-90-054). NCI Q66B-2242-Y: W side Canoe I., 10°20.6'S, 142°06.4'E, 4m depth, 6.v.1987, coll. NCI, SCUBA. - CAIRNS SECTION: NTM Z3165, 3166, 3167, 3168 (fragments): Outer slope, reef front, Blue Lagoon, Lizard I., 14°40'S, 145°28'E, 10-20m

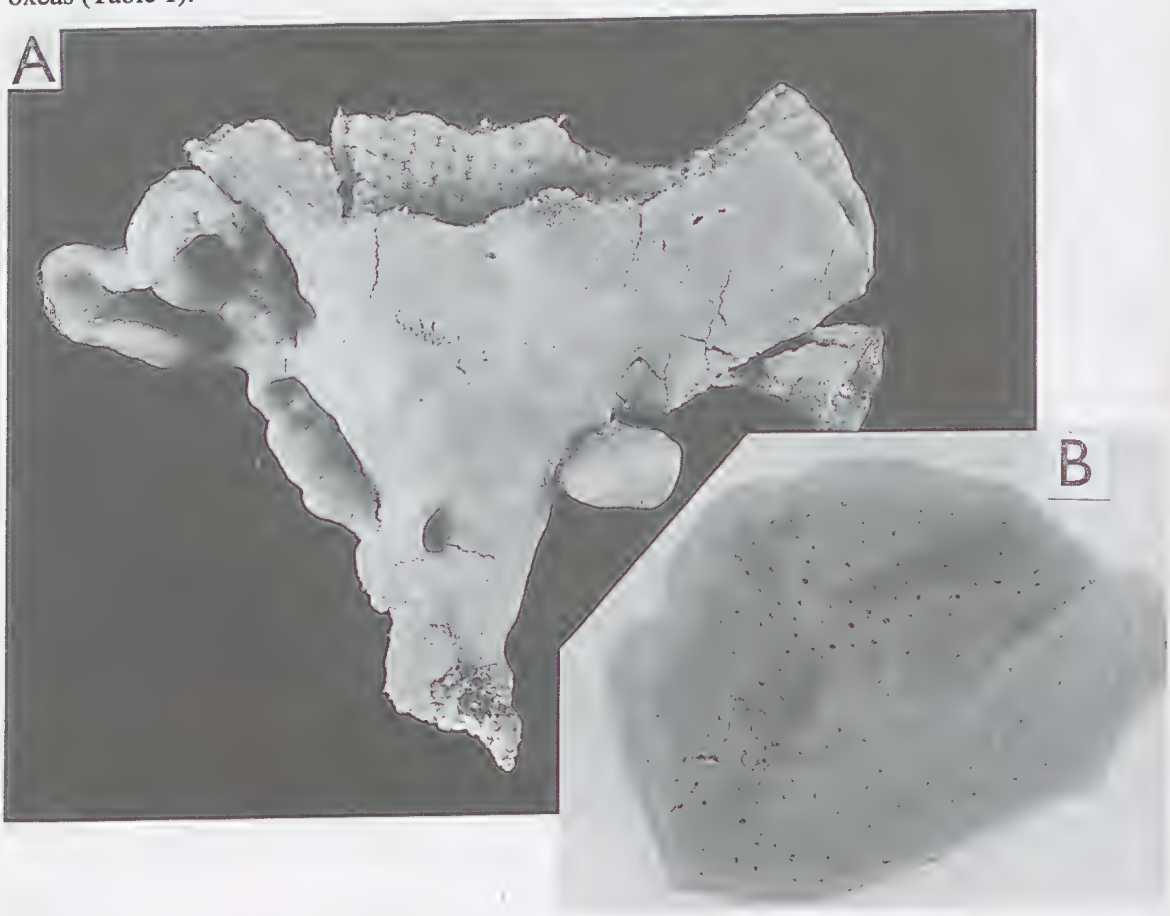


FIG. 12. *Cymbastela cantharella*. A, specimen (NTM Z3872). B, close up view of interior surface of cup (specimen NTM Z3869).

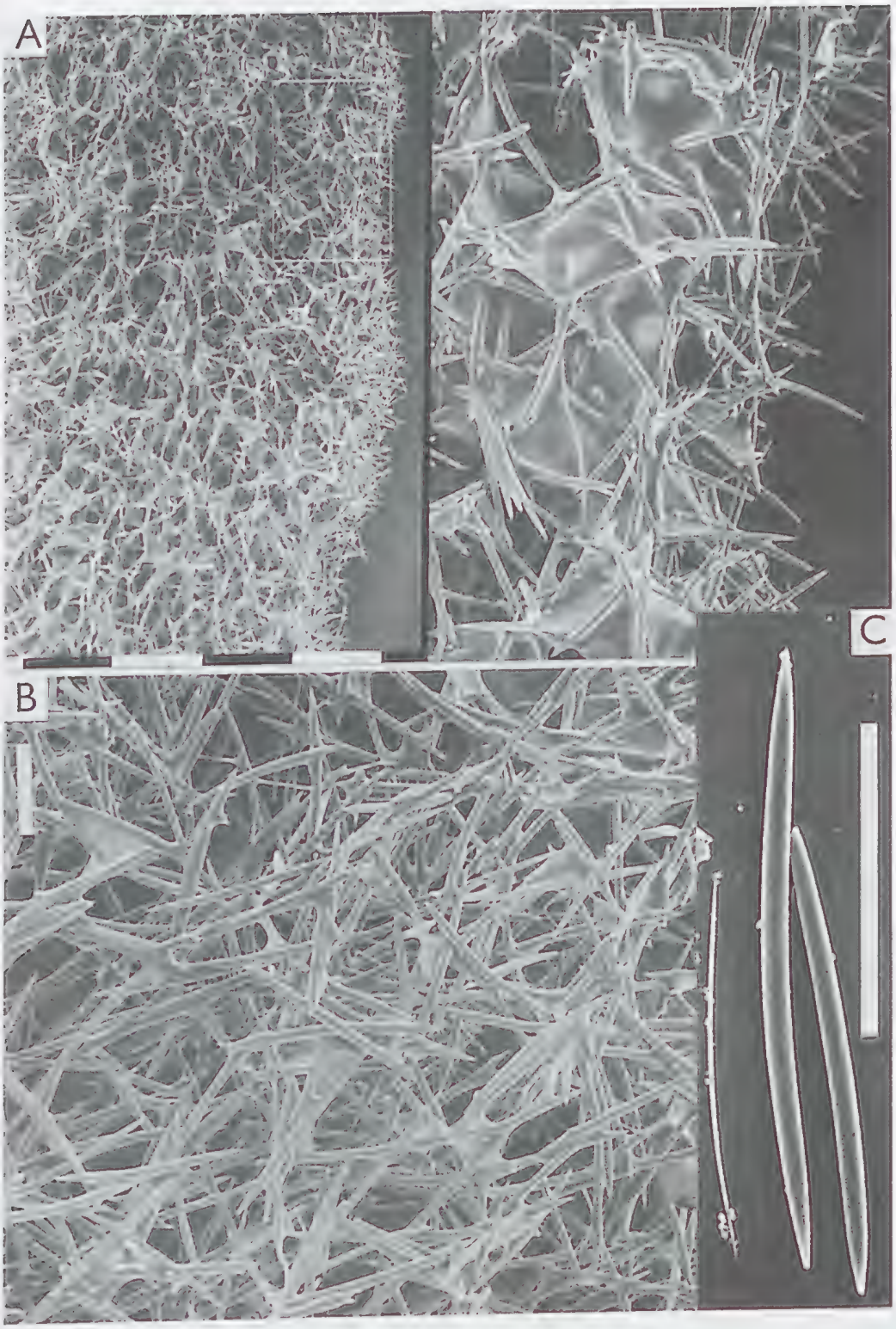


FIG. 13. *Cymbastela cantharella*. A, SEM of skeleton (specimen NTM Z3872) (scale=500μm; left magnified 106 times, right magnified 566 times). B, peripheral skeletal architecture (scale=100μm). C, oxeas, including juvenile form (specimen ORSTOM RA1279) (scale=100μm).

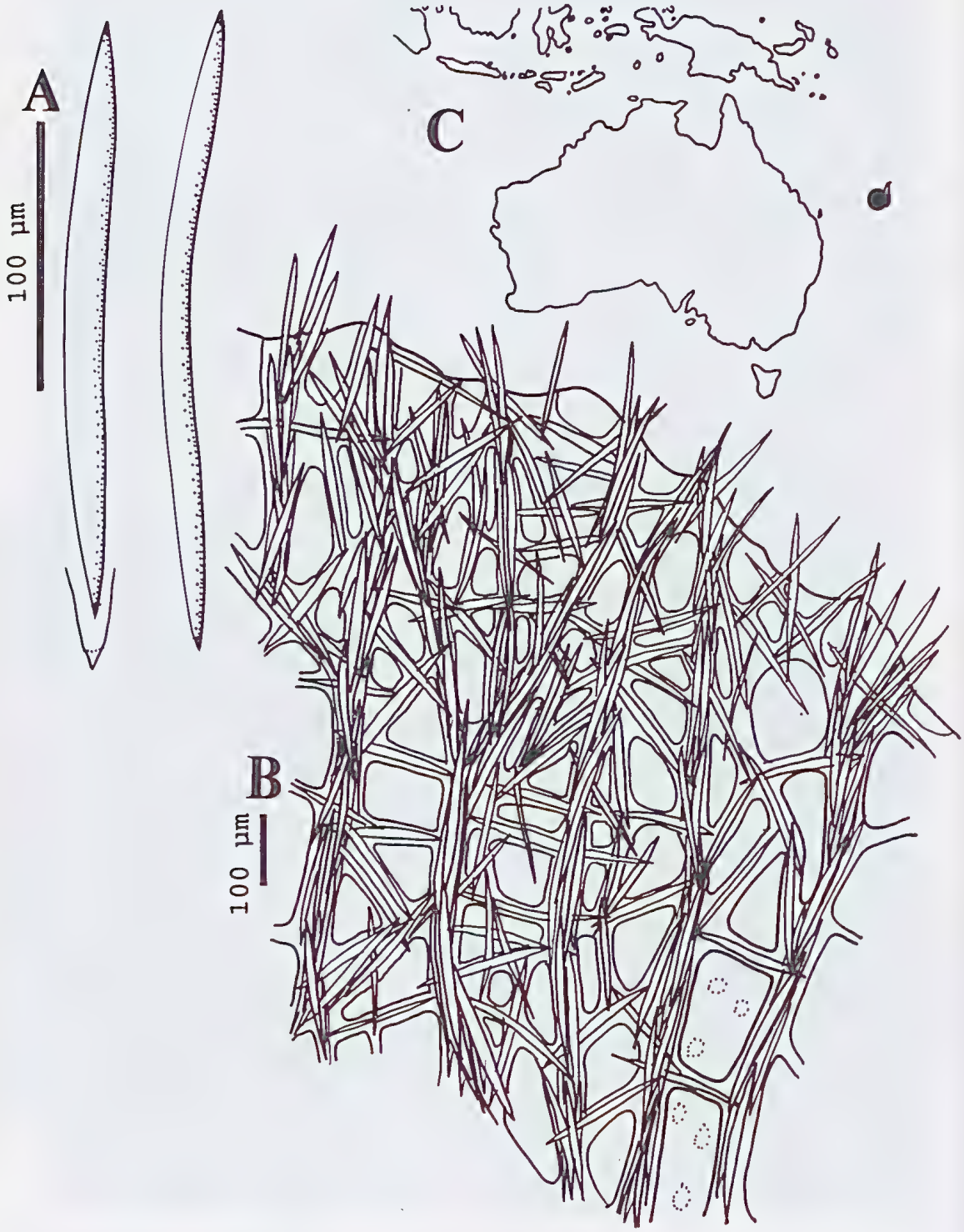


FIG. 14. *Cymbastela cantharella*, specimen (NTM Z3872). A, spicules. B, section through peripheral skeleton. C, known distribution.

depth, 1987, coll. A.W.D. Larkum et al. (ref. PC341T, PC342T, PC344T, PC345T, respectively). NCI Q66C-0260-W: N end Bowden Reef, off Townsville, 19°2.06'S, 147°55.89'E, 14m depth, 3.ii.1987, coll. NCI, SCUBA. - CENTRAL SECTION: AIMS RA3-PR (fragments NTM Z2735, QM G300012): Davies Reef, Townsville region, 18°50'S, 147°39'E, depth unknown, 17.viii.1982, coll. C.R. Wilkinson (stn Don.214). - CAPRICORN SECTION: NCI Q66C-1766-L (fragments NTM Z3509, QM G300008): 100m NW of small rocky point at embayment edge, NW Brampton Island, Whitsunday Islands Group, Mackay region, 20°48.0'S, 149°15.0'E, 12m depth, 07.xi.1988, coll. NCI, SCUBA (stn DON-0272). NCI Q66C-0816-A: W end Deloraine I., Whitsunday Is Group, Mackay region, 20°09'S, 149°04'E, 20m depth, 10.xi.1987, coll. NCI, SCUBA.

SUBSTRATE AND DEPTH RANGE

Coral reef substrates, including lagoon, sloping fringing reef, irregular coral boulders with muddy sand between, gorgonian beds, and also areas of high sedimentation. Depth range extends from subtidal to 20m.

GEOGRAPHICAL DISTRIBUTION

Northern, central and southern sections of the Great Barrier Reef, Queensland (Fig. 17C).

ETYMOLOGY

The species name refers to the restricted distibution of all material so far described, the sponge being found exclusively on coral reefs.

DESCRIPTION

Shape: Large vase-shaped, cup-shaped or simply lamellate growth forms, usually with large marginal opening, or sometimes nearly flattened completely against substrate, 80-170mm high, up to 350mm maximum marginal diameter. Usually attached to substrate by short stalk, up to 30mm high, 25mm diameter, sometimes lamellae are direct outgrowths of the basal attachment. Lamellae relatively thick, lobate, 8-15mm thick excluding lateral projections (Fig. 15).

Surface features: External, exhalant, surface optically smooth, relatively even, with or without bumps, ridges and lateral growths. Internal, inhalant, surface relatively uneven, often with concentric striations and ridges, or with irregular bumps, lobate growths and depressions on lamella walls, typically with small digitate or lobate projections at centre of cup. Occurrence and development of surface outgrowths, on both interior and exterior surfaces of lamellae is highly variable. Oscules small, 0.5-2mm diameter, dispersed on tips of microconules or ridges on interior surface of cups, subdermal canals visible below slightly translucent ectosome (Fig. 15C-D).

Colour: Live colouration typically mottled olive-brown (Munsell 7.5YR 5/4), olive-green (5Y 6/6) with maroon-brown tinge externally (5R 4/2), green (7.5GY 3/4) or olive-green internally (2.5GY 5/4). Colour in ethanol white or greenish-white.

Texture: Compressible, difficult to tear, rough exterior texture.

Ectosome: Ectosome microscopically hispid, with specialised skeleton. Subectosomal skeleton ascending, plumose, produced by pauci- or multispicular tracts of larger, choanosomal oxeas running at right angles to surface, overlain by specialised ectosomal skeleton of tangential, multispicular brushes made up of smaller ectosomal oxeas. Specialised dermal skeleton markedly plumose, mostly orientated tangentially or paratangentially to surface (Figs 16, 17B).

Choanosome: Choanosomal skeleton with only slight axial condensation, with axial and extra-axial components only slightly differentiated (Fig. 17B). Axial region predominantly radial-plumose, less markedly plumo-reticulate, with skeletal lines mostly directed longitudinally through lamellae, but gradually ascending towards peripheral skeleton; extra-axial skeleton more-or-less radial-plumose, with multispicular ascending spongin fibres interconnected by paucispicular transverse fibres (Fig. 16). Spongin fibres well formed but only very lightly invested with spongin, 75-110μm diameter. Fibre reticulation forms elongate oval to elliptical meshes, 85-350μm diameter, relatively similar in diameter between axial and extra-axial regions; choanocyte chambers relatively large, oval, 90-210μm diameter. Ascending fibres cored by multispicular tracts of larger choanosomal oxeas, whereas transverse fibres uncored or with uni- or paucispicular skeletal lines. Mesohyl matrix reinforced with moderate quantities of collagen. Very thin, smaller oxeas, similar in length to those on surface skeleton are dispersed throughout the mesohyl, possibly juvenile forms of larger choanosomal oxeas.

Spicules (refer to Table 1 for dimensions): Choanosomal oxeas thick, slightly curved at centre, typically symmetrical, occasionally anisoxeote, with hastate-rounded or slightly pointed, usually very faintly telescoped ends. Ectosomal oxeas thin, mostly straight, fusiform, with sharply pointed, rarely telescoped ends (Fig. 17A).

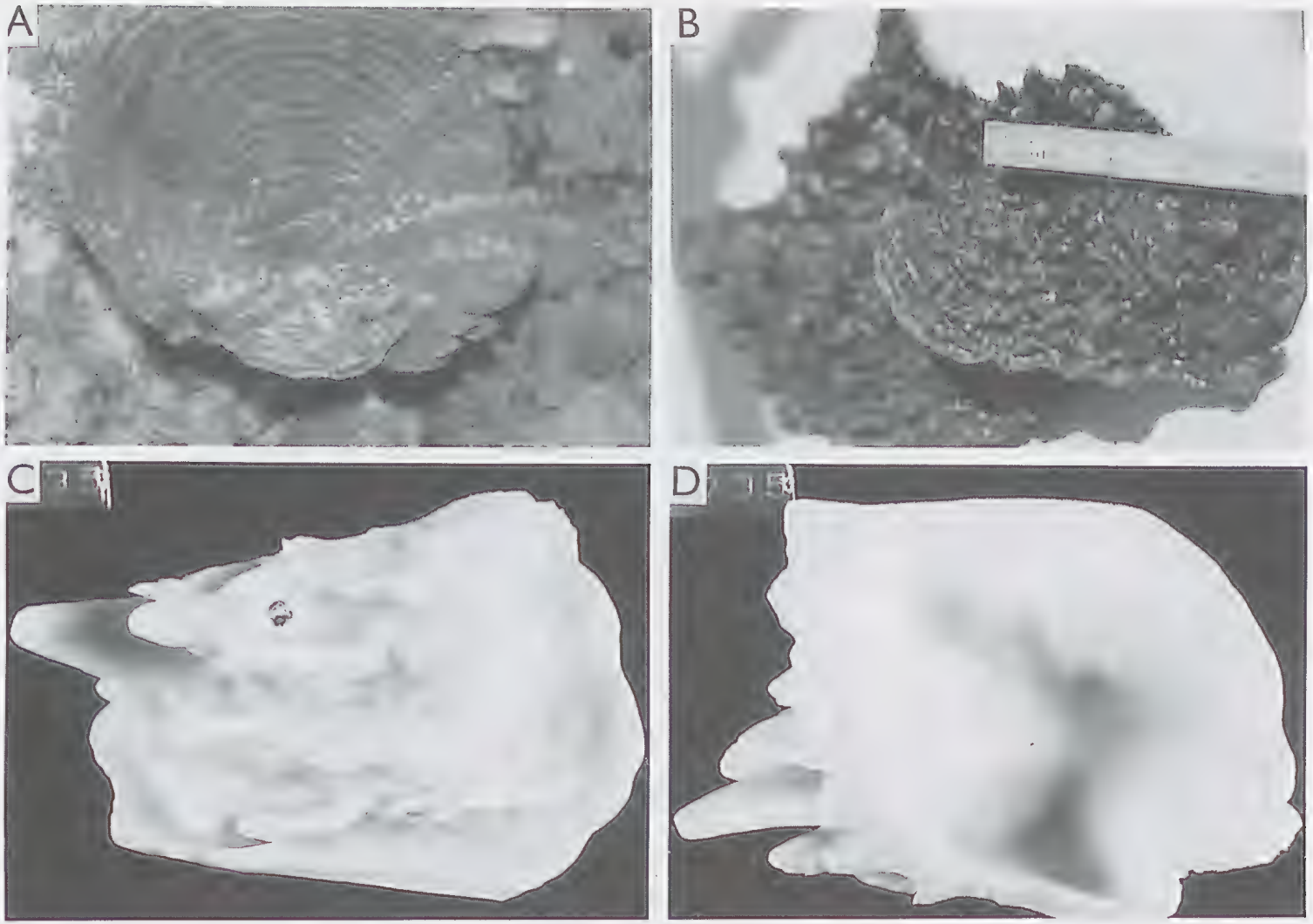


FIG. 15. *Cymbastela coralliophila* sp.nov. A, specimen in situ (NTM Z2735; photo C. Wilkinson). B, specimen (NTM Z3166), showing interior surface of lamellae in live state. C-D, specimen (NTM Z2735), showing close up view of exterior (C) and interior (D) surfaces of lamellae, in preserved state.

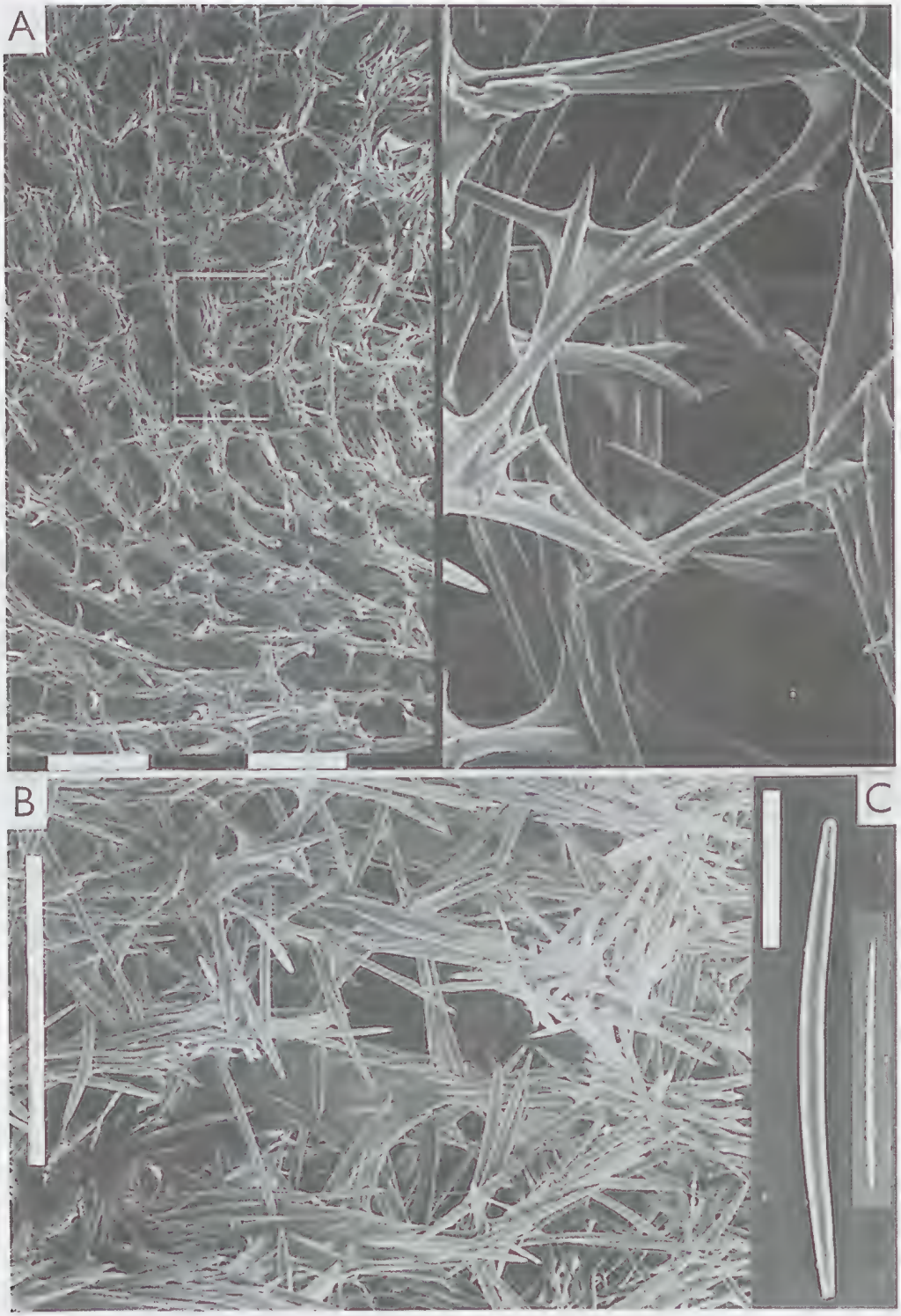


FIG. 16. *Cymbastela coralliophila* sp.nov. A, SEM of skeleton (specimen NTM Z2735) (scale=500μm; left magnified 19.5 times, right magnified 93 times). B, peripheral skeletal architecture (specimen NTM Z3509) (scale=500μm). C, two sizes of spicules (scale=100μm).

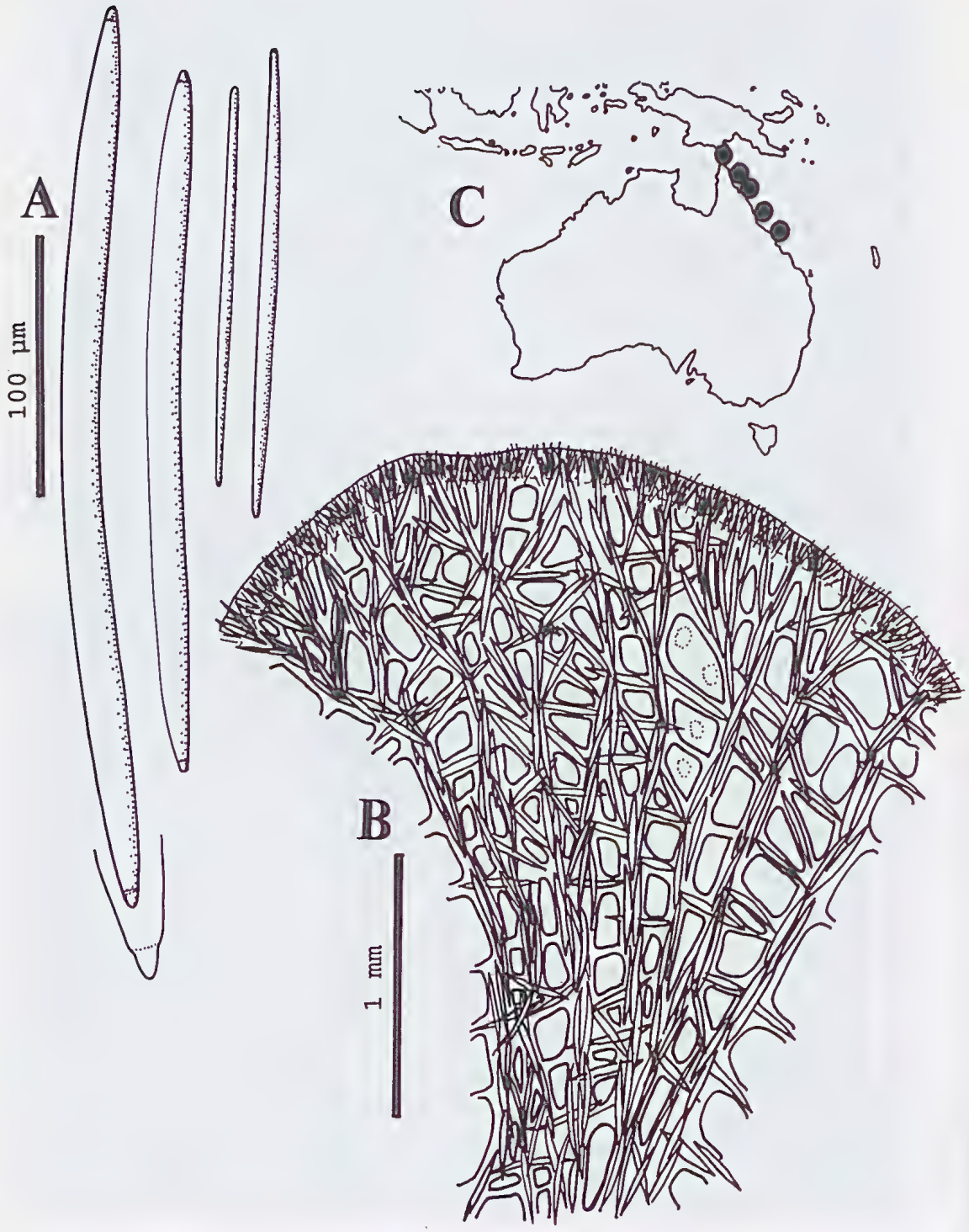


FIG. 17. *Cymbastela coralliophila* sp.nov. (specimen NTM Z2735). A, choanosomal and ectosomal spicules. B, section through peripheral skeleton. C, known distribution.

Reproduction

Oviparous, with synchronous release of eggs and sperm (A. Ayling, pers. comm.).

Associations

Sponges tested chlorophyll positive, and it is likely that the species' live pigmentation is partially or entirely produced by cyanobacterial symbionts. Several specimens also had numerous zoanthids on upper and lower surfaces, and barnacles (*Acasta* sp.) embedded within the mesohyl.

Remarks

Cymbastela coralliophila has been recorded frequently from the Great Barrier Reef, but until now it has remained undescribed.

The species conforms with Burton's (1931) interpretation of the genus *Axinyssa*, as distinct from his nominal genus *Pseudaxinyssa*, in that it contains two distinct size classes of oxeas, the smaller found predominantly on the surface, the larger forming the structural skeleton. On the other hand, the very close similarities in growth form, skeletal architecture and spiculation that exist between this species and the other Australasian lamellate *Cymbastela* suggests that this feature is not important above the species level of classification. *Cymbastela coralliophila* also differs from other members of the genus, as construed here, in having an almost flattened, usually relatively large cup-shaped growth form, with flabellate lamellae. The skeletal structure is most similar to *C. cantharella*, with the radial-plumose skeletal tracts predominant over the reticulate component of the skeleton, and with only minor differences between the axial and extra-axial regions. The species are contrasted further in Table 1.

Cymbastela marshae sp.nov.

(Figs 18-20, Table 1)

Material Examined

Holotype: NTM Z2876: Northern edge of Pelsar Islets, Houtman-Abrolhos Is, WA, 28° 47.6'S, 114° 00.7'E, 25m depth, 09.vii.1987, coll. J.N.A. Hooper, USSR RV 'Akademik Oparin', SCUBA (stn JH-87-001).

Other Material: Houtman-Abrolhos Is, WA - NTM Z2901 (fragment QM G300005): Pelsar Islets, 28°47.2'S, 113°58.5'E, 22m depth, 10.vii.1987, coll. J.N.A. Hooper, USSR RV 'Akademic Oparin', SCUBA (stn JH-87-002). NCI Q66C-4198-F: 1.5 km N of northern point, West Wallabi I., Wallabi Group, 28°25.7'S, 113°42.0'E, 8m depth, 12.ix.1990, coll. NCI, SCUBA.

Substrate and Depth Range

Growing at base and on reef slope of *Acropora* and *Seriatopora* coral reef, in sand, silt or rock substrates, in *Turbinaria* zone, 8-25m depth.

Geographical Distribution

Known only from the Houtman-Abrolhos Islands, WA (Fig. 20C).

Etymology

Named after Mrs Loisette Marsh, Curator of Marine Invertebrates, Western Australian Museum, Perth, in respect of her dedication to the study of the marine fauna of Western Australia.

Description

Shape: Thin, irregularly lamellate lobes forming asymmetrical vases, or symmetrical cup-shaped sponges, 125-255mm high, 120-235mm wide at apex of lamellae, with thin lamellae, 2-6mm maximum width, attached directly to substrate by a basal attachment, without a basal stalk (Fig. 18).

Surface features: Smooth, relatively even surface. Exterior surface with few low, irregular bumps, shallow depressions and concentric ridges, with or without horizontal lamellate projections growing on side of exterior surface. Interior, oscular surface of lamellae smooth, with concentric ridges, few low, irregular conules or depressions, sometimes with secondary lamellae or whole cups growing within interior surface. Very small oscules scattered over interior of cups, up to 1.5mm diameter.

Colour: Olive-green and maroon alive (Munsell 5Y 5/4 and 2.5R 4/8), evenly pigmented on exterior and interior surfaces, beige in ethanol.

Texture: Firm, flexible, slightly compressible texture, smooth to touch, difficult to tear.

Ectosome: Membraneous, without specialised skeleton, with plumose brushes of choanosomal oxeas protruding through surface for up to 170μm, consisting of 2-8 spicules per bundle. Ectosome with thin layer of darker pigmented granular collagen, 40-70μm wide, with heavy concentrations of microalgae, and also with a thin, disorganised paratangential layer of choanosomal oxeas scattered between erect, protruding ectosomal brushes. Subectosomal skeleton cavernous, predominantly plumose, slightly reticulate, with reticulate component decreasing closer to periphery (Figs 19, 20B).

Choanosome: Choanosomal skeleton plumoreticulate, with axial skeleton dominated by longitudinal tracts running through lamellae, gradually ascending towards surface, becoming

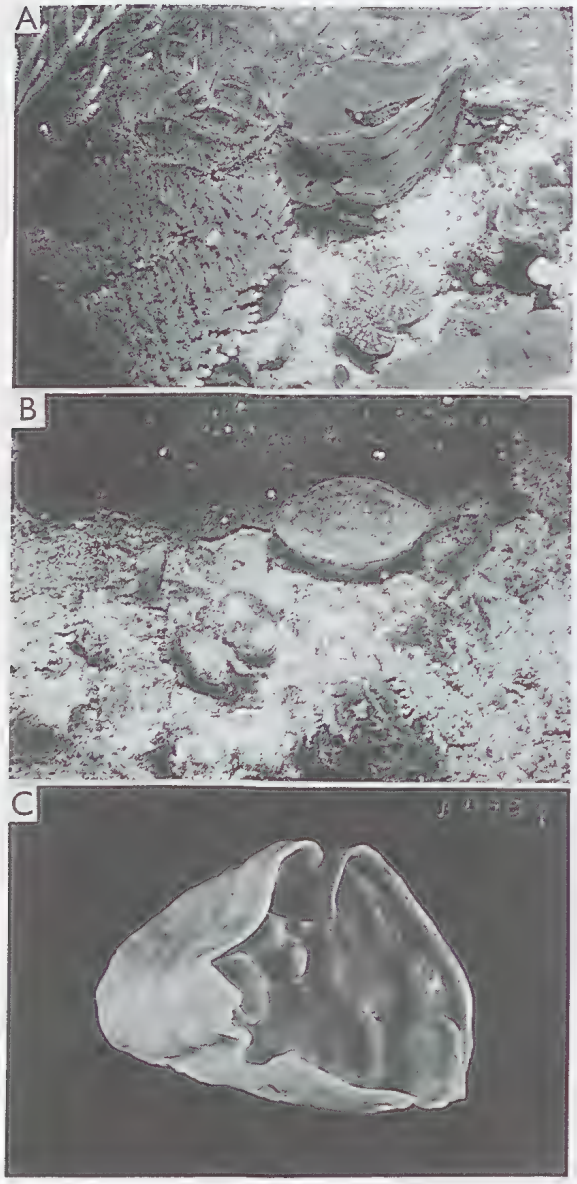


FIG. 18. *Cymbastela marshae* sp.nov. A, holotype (NTM Z2876), in situ. B-C, specimen (NTM Z2901) in situ (B) and preserved (C).

nearly plumose near peripheral skeleton (Fig. 20B). Axial skeleton slightly condensed at centre of lamella with reasonably well differentiated axial and extra-axial regions. Spongin fibres well developed, with obvious differentiation between multispicular primary (longitudinal and ascending) and uni- or paucispicular secondary (transverse, connecting) elements (Fig. 19). Primary fibres 30-80μm diameter, rarely fully cored with megascleres, secondary fibres much smaller, 15-25μm diameter, usually with greater silica to spongin ratio. Fibre meshes elongate oval or diamond-shaped in axis, 70-105μm maximum diameter, generally more cavernous in periphery, up to 150μm maximum diameter. Choanocyte chambers small, up to 45μm diameter. Mesohyl matrix only lightly invested with collagenous spongin, with abundant microalgae scattered throughout.

Spicules (refer to Table 1 for dimensions): Oxeas relatively short, slender, slightly curved at centre, with tapering, fusiform, usually telescoped points (Fig. 20A).

ASSOCIATIONS

Although not analysed chemically (acetone extracted), the olive-green and maroon pigments of this species are probably due to the presence of cyanobacteria scattered within the mesohyl. Each of the specimens examined was also found to have several barnacles boring within the lamella wall, near the base of the sponge.

REMARKS

This species is most closely related to *C. stipitata* in skeletal structure, as the plumose longitudinal and ascending primary tracts dominate the skeletal architecture. Both species have condensed axial regions and differentiated axial and extra-axial skeletons, with well developed plumose ectosomal skeletons. *Cymbastela marshae* also has a cavernous subdermal region, and spicules are about half the dimensions of those in *C. stipitata* (Table 1). The present species is close to *C. coralliophila* in growth form, lamella thickness and surface pigmentation.

Cymbastela notiaina sp.nov.
(Figs 21-23, Table 1)

MATERIAL EXAMINED

HOLOTYPE: SAM TS4025 (fragments NTM Z1623a, QM G300007): Precise locality unknown, Gulf of St Vincent, SA, 34°33-45'S, 137°57'-138°10'E, depth and date of collection unknown.

SUBSTRATE AND DEPTH RANGE

Unknown.

GEOGRAPHICAL DISTRIBUTION

South Australia (Fig. 23C).

ETYMOLOGY

Greek, *notos*, south; *notiaina* refers to the southern distribution of this species.

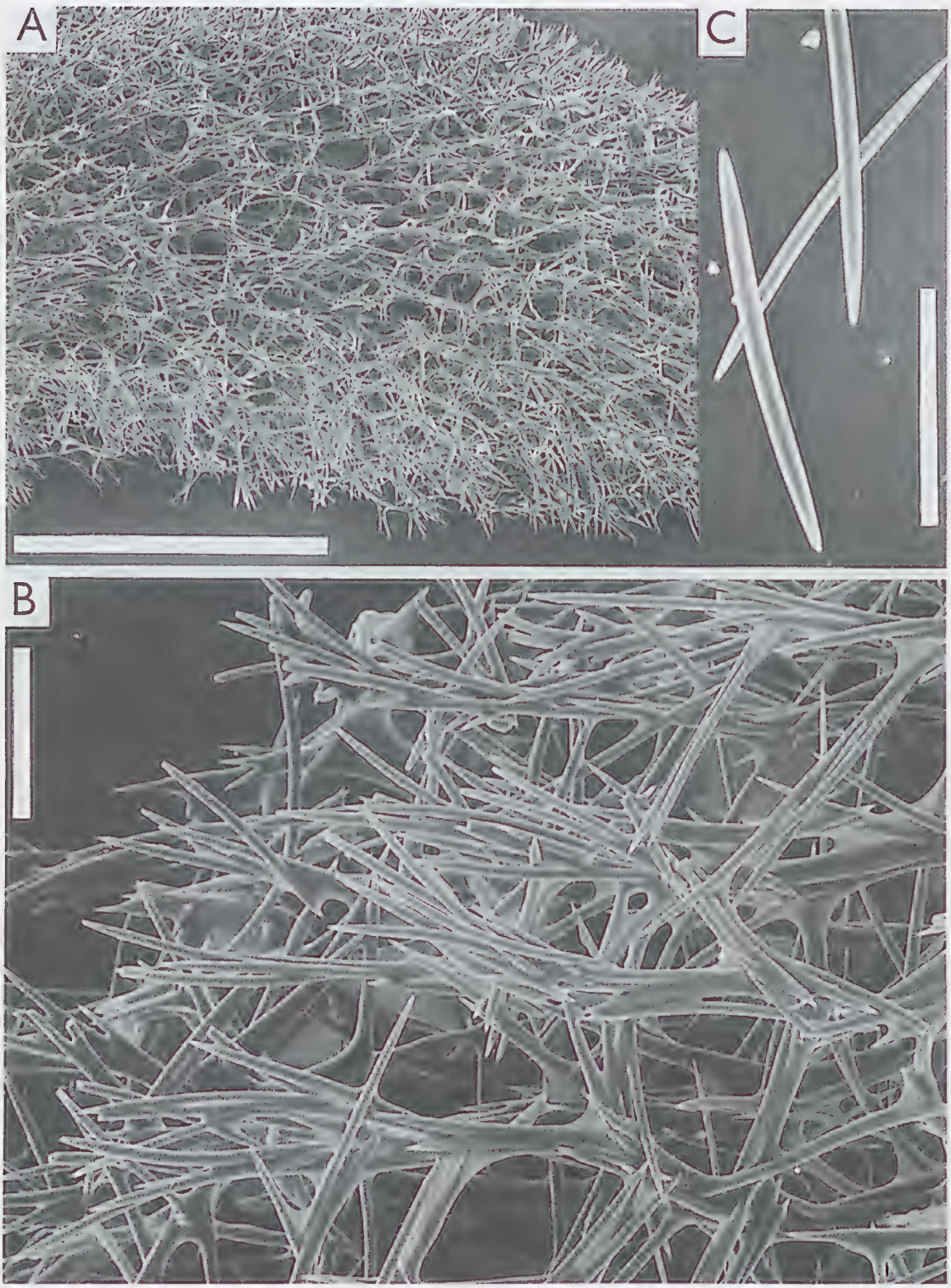


FIG. 19. *Cymbastela marshae* sp.nov. A, SEM of skeleton (specimen (NTM Z2901) (scale=1mm). B, peripheral skeletal architecture (scale=100μm). C, oxeas (scale=100μm).

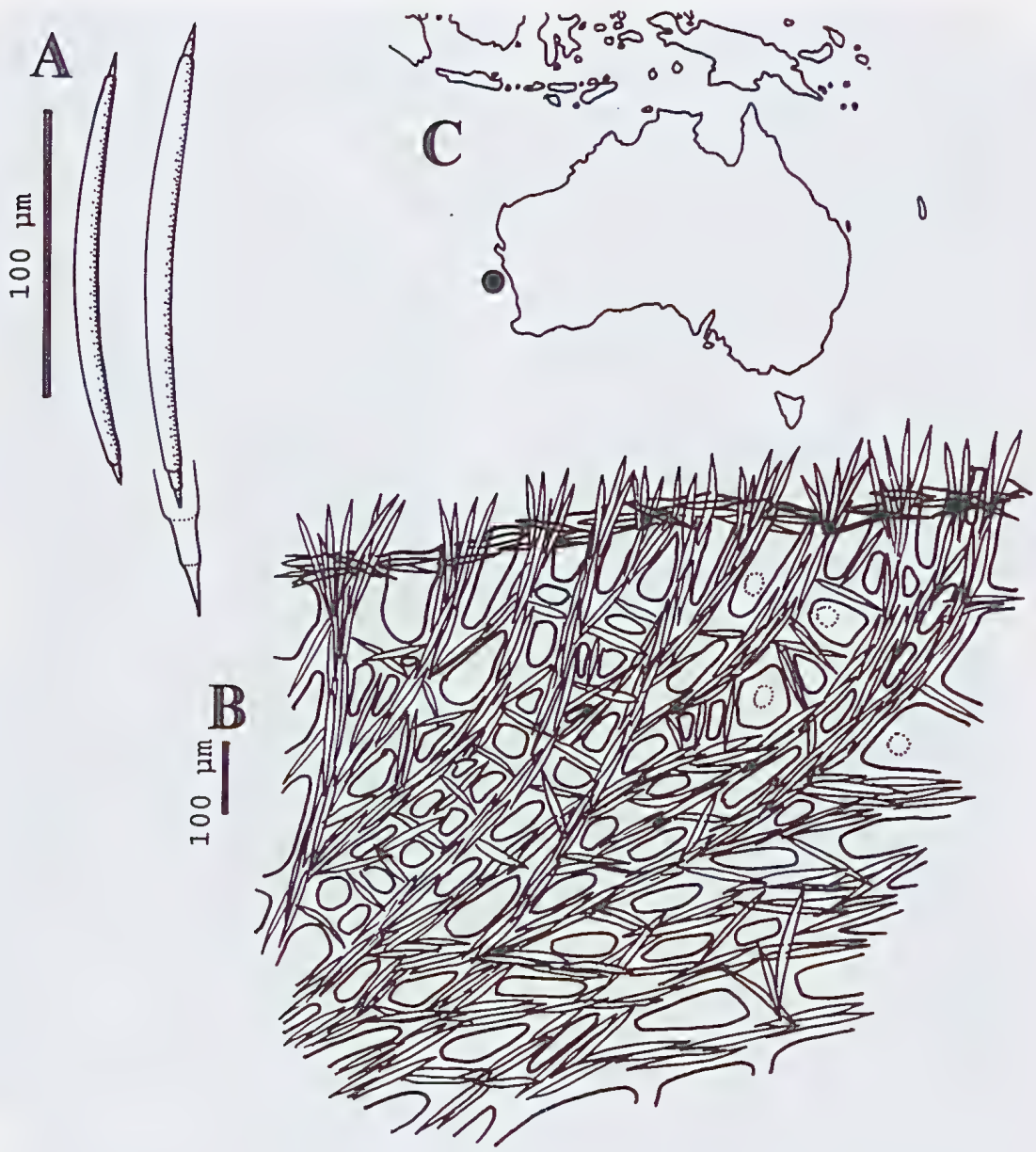


FIG. 20. *Cymbastela marshae* sp.nov. A, spicules. B, section through peripheral skeleton. C, known distribution.

DESCRIPTION

Shape: Small, symmetrical vasiform sponge, 96mm high, 125mm maximum diameter at apex of cup, on short thick stalk with expanded basal attachment, 12mm long, 35mm diameter, and thin lamellae, 3-5mm thick (Fig. 21).

Surface features: Interior and exterior surfaces optically even, without conules, buttresses or other lateral growth projections. Exterior surface has longitudinal, concentrically striated ridges. Oscules minute, less than 1mm diameter, dispersed over interior surface of cup.

Colour: Live colouration unknown, olive-brown in ethanol.

Texture: Firm, flexible, compressible in preserved state, smooth to touch.

Ectosome: Ectosome optically smooth, membraneous, slightly hispid due to protruding

spicule brushes, slightly microconulose, with microconules corresponding to surface brushes. Ectosomal skeleton distinctly plumose, with bundles of 2-15 choanosomal spicules protruding up to 90μm from surface, perched on ends of ascending extra-axial skeletal tracts (Figs 22, 23B).

Choanosome: Choanosomal skeleton with no axial condensation, and only slightly differentiated axial and extra-axial regions (Fig. 23B). Skeleton almost regularly reticulate at the core, with oval meshes, 70-120μm diameter, formed by multispicular spongin fibres, both longitudinal and connecting. Skeleton plumo-reticulate towards periphery, with ascending multispicular fibres predominant over uni- or paucispicular transverse connecting fibres. Spicules form plumose brushes close to, and protruding from, surface. Fibre meshes in peripheral skeleton elongate-rectangular, slightly larger than in axis, 100-140μm diameter (Fig. 22). Spongin fibres relatively large, 40-85μm diameter, partially but never fully occupied by spicules. Mesohyl matrix lightly reinforced with collagen, choanocyte chambers oval, 40-90μm diameter.

Spicules (refer to Table 1 for dimensions): Oxeas almost vestigial by comparison with other species, poorly silicified, very thin, small, only slightly curved at centre, with prominently telescoped ends and rounded tips (Fig. 23A).

Associations

No symbiotic cyanobacteria were seen in the holotype.

Remarks

This species is presently known only from the holotype described above, although a small fragment from a second specimen exists in the SAM collection (SAM TS4058 [section/fragments NTM Z1665, QM G300011], from Port Noarlunga, SA), may also belong to the species. *Cymbastela notiaina* is easily differentiated from other taxa by its regular, nearly completely reticulate choanosomal skeleton, the small size of megascleres (Table 1), and the telescoped, rounded (strongylote) points of oxeas, unlike any other species.

DISCUSSION

Taxonomy

Small differences in field characteristics, such as live colouration, growth form, surface features, including outgrowths on the surface and lamellae thickness, as described above for each species, can serve as field identifiers for the seven known species of *Cymbastela.* However, morphological differences seen in preserved material, which correlate with these species boundaries are less obvious. Certainly, in terms of general skeletal structure and spicule geometry the genus is relatively homogenous, and it is only through small but significant differences in a small number of skeletal characters that species can be reliably differentiated. These characters, which are shown to be most important, include spicule length, spicule geometry, including the presence or absence of telescoped ends on spicules, and degree of silicification, and the relative, proportional development of the axial and extra-axial skeletons. On this basis it was possible to construct a key to species of *Cymbastela* (see above), with emphasis given to the morphology of preserved specimens. Thus, whereas the characters used to differentiate species in this key may seem trivial, these differences correspond with more obvious field characteristics, many of which are no longer visible in the preserved material.

It was also noted that, in general, species could be separated by their mean spicule dimensions. Generally, the relative size of oxea megascleres decreases with increasing latitude (Fig. 24A-B), such that species from low (tropical) latitudes (*C. stipitata, C. coralliophila, C. vespertina*) have larger oxeas than those species from higher latitudes (*C. cantharella, C. marshae, C. notiana*). *Cymbastela concentrica*, which has a wide latitudinal distribution (14-26°S; Fig. 24B), also has a relatively wide range of spicule dimensions (Fig. 24A, symbol 5).

Biogeography

Although it is possible that more extensive sampling along the cool temperate Australasian coastline will reveal additional species, *Cymbastela* is presently known to be predominantly a shallow water, tropical or subtropical genus, usually associated with coral substrates. The genus appears to be endemic to the Indo-west Pacific, extending only as far as New Caledonia (longitude 166°E) to the east, and to the Houtman-Abrolhos Islands (113.5°E) to the west, and so far there are no confirmed records of the genus from either Indonesia (unpublished *Siboga* and *Snellius II* collections, R.W.M. Van Soest, pers.comm.) or New Zealand (personal observations). However, it is possible that misidentified specimens of *Cymbastela* exist in other museum collections. The genus is certainly not present in the published

collections of Hentschel (1912), from the Aru and Kai Islands, southeast Indonesia (ZMB collections), in which close similarities with the northwest Australian sponge fauna can be seen (e.g. Hooper, 1991).

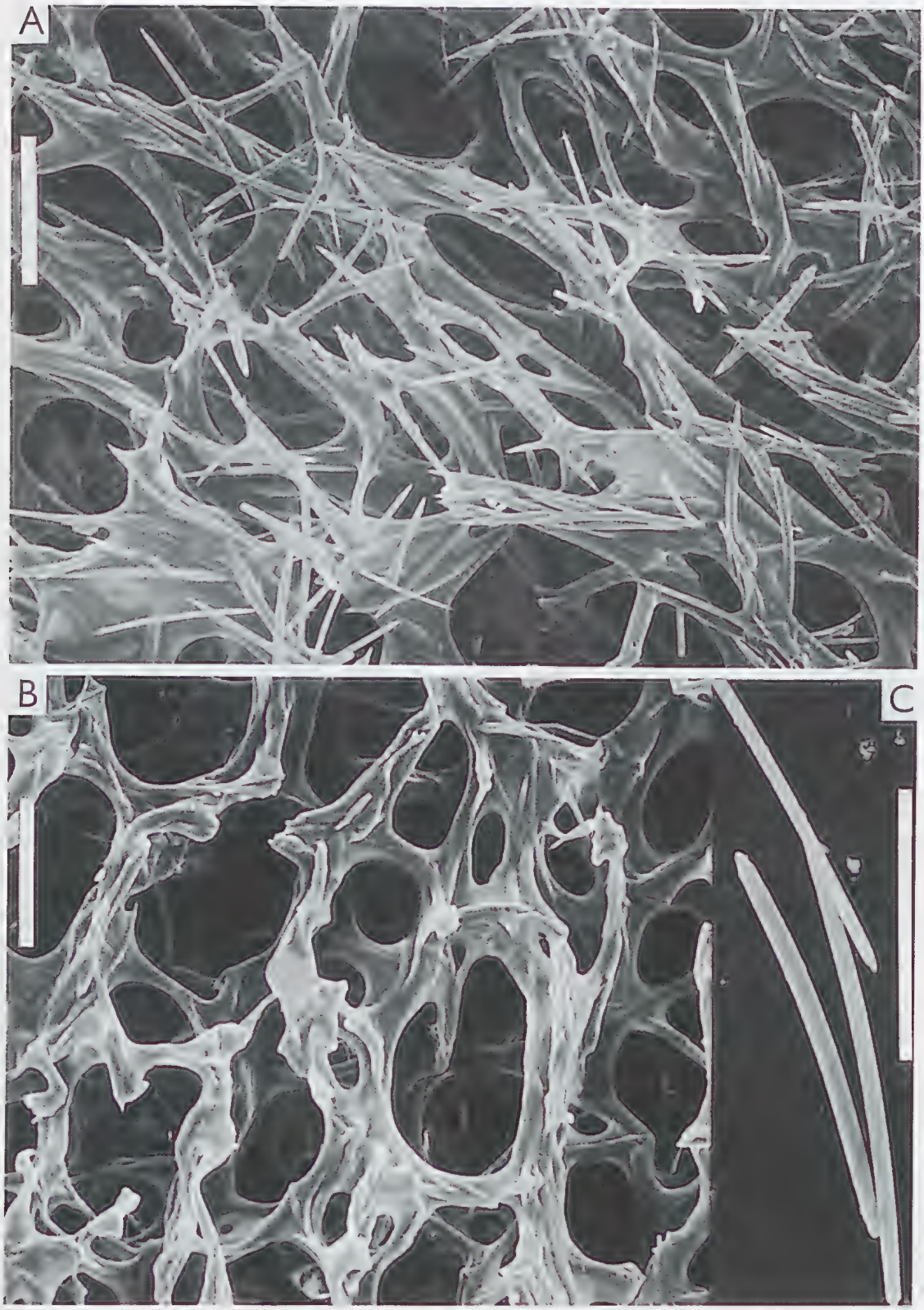
Three species of *Cymbastela* have restricted, allopatric distributions (*C. cantharella, C. marshae, C. notiaina*; Fig.25), whereas on the northwest and northeast coasts of Australia there are two groups of more-widely distributed, sympatric species. Within the northwestern area of sympatry (Fig. 25), there is some evidence of niche separation between the two populations, *C. stipitata* and *C. vespertina*. The former species has a predominantly shallow water distribution, found mostly in the intertidal region and only exceptionally down to 19m depth, whereas *C. vespertina* is found mostly in deeper water, only rarely above 8m depth. Population characteristics of the northeast Australian sympatric species, *C. coralliophila* and *C. concentrica*, have not yet been determined, and the latter species, in particular, is still poorly known.

PHYLOGENY

Under Van Soest et al.'s (1990) interpretation of the existing family Axinellidae *Cymbastela* would be placed with a group of genera having axially condensed and extra-axially plumo-reticulate skeletons, for example *Auletta, Axinella, Axinosia, Homaxinella, Phakellia, Pseudaxinella, Reniochalina* and *Teichaxinella*, which Van Soest et al. (1990) retained in a newly defined concept of family Axinellidae. Of these genera *Cymbastela* is most closely related to *Axinella*. Conversely, they placed the genus *Axinyssa*, previously considered to be a close relative of '*Pseudaxinyssa*' s.l. (= *Cymbastela*), in a redefined family Halichondriidae since it has poorly developed spicule tracts. This group would contain 'axinellid' genera such as *Axinyssa* and *Amorphinopsis*, several genera previously in-

FIG. 21. *Cymbastela notiaina* sp.nov. A, holotype (SAM TS4025).

FIG. 22. *Cymbastela notiaina* sp.nov. A, SEM of peripheral skeleton (holotype, SAM TS4025) (scale=100μm). B, axial skeleton (scale=100μm). C, spicules with telescoped ends (scale=50μm).


A
B
C

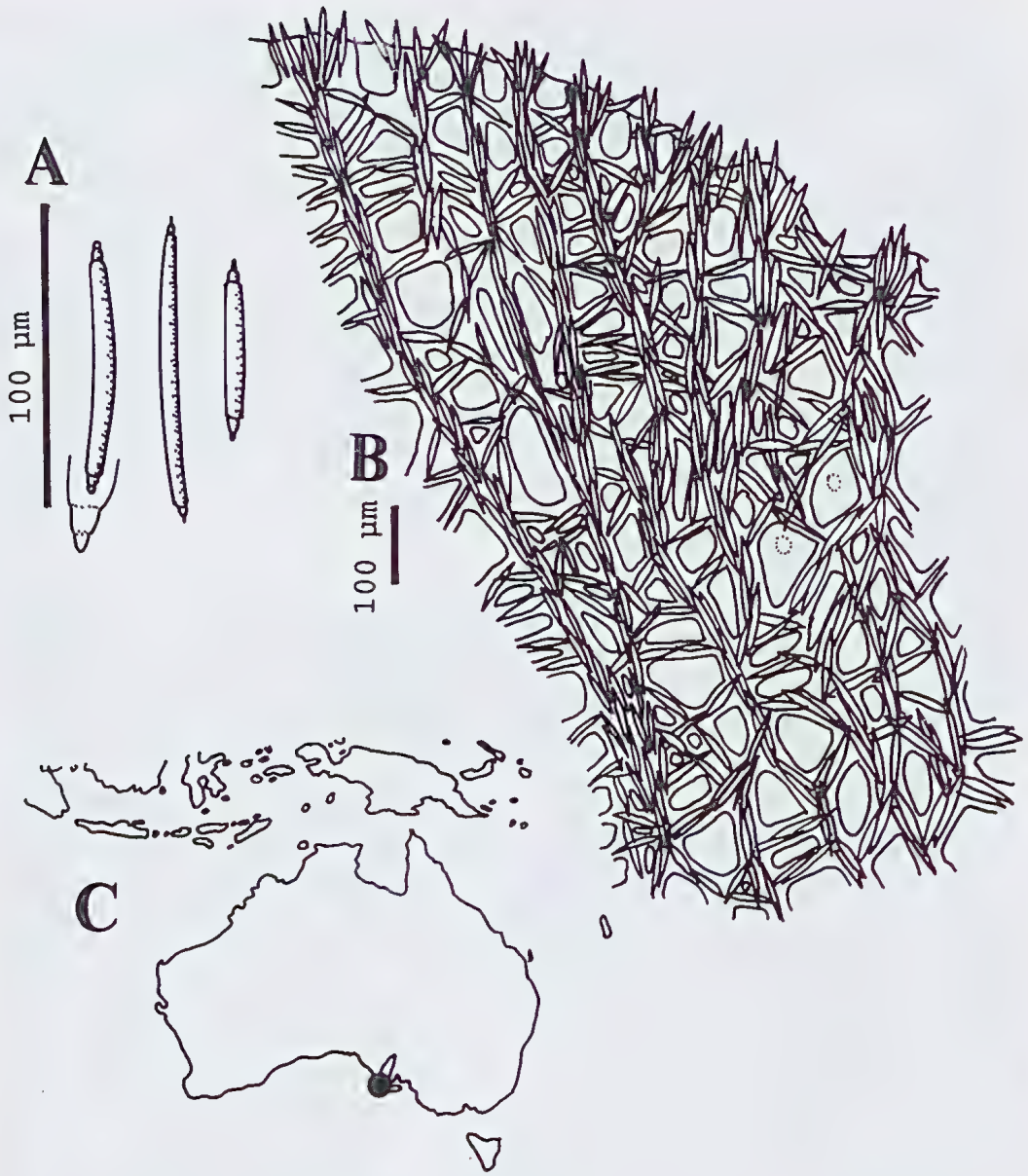


FIG. 23. *Cymbastela notiaina* sp.nov. A, spicules. B, section through peripheral skeleton. C, known distribution.

cluded in Desmoxyidae (e.g. *Myrmekioderma*), and other genera traditionally associated with the halichondrids and hymeniacidonids (e.g. *Ciocalypta*, *Hymeniacidon*). A third group of 'axinellids' with dendritic skeletons (e.g. *Acanthella*, *Dictyonella*, *Scopalina*), were removed to the new family Dictyonellidae. The fourth family, Desmoxyidae, wäs also previously aligned with the Axinellida, differing from other 'axinellids' in having a reticulate-fasciculate choanosomal skeleton and a fleshy corrugated surface (Van Soest et al., 1990:18). It contained several desmoxyid genera (e.g. *Higginsia*), but excluding *Myrmekioderma*, as well as some Axinellidae (e.g. *Ptilocaulis*). We consider that these new family divisions proposed by Van Soest et al.

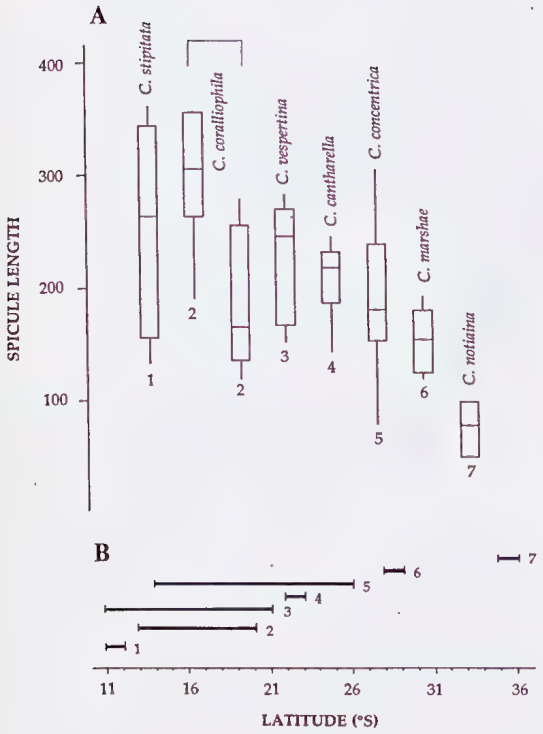


FIG. 24. A, Comparison in spicule lengths (μm) between seven species of *Cymbastela*, and B, latitudinal differences in distribution for each species. Box-and-whisker plots show the range of spicule dimensions (i.e. 'whiskers'), the median values (i.e. 50% of data values, between lower and upper quartiles - open boxes), and the average length of oxeas for each species (i.e. mid-range bars). Key to species codes: 1, *C. stipitata*; 2, *C. coralliophila* (large and small oxeas); 3, *C. vespertina*; 4, *C. cantharella*; 5, *C. concentrica*; 6, *C. marshae*; 7, *C. notiaina*.

(1990) have some merit over the existing, confused system for Axinellidae - Halichondriidae - Hymeniacidonidae, but we are uncertain whether all these 'axinellids' and 'halichondrids' have a monophyletic origin, and we leave open the question of their ordinal classification for the time being. Further evidence from molecular and genetic nature may be useful in evaluating these relationships in an objective context.

ACKNOWLEDGEMENTS

We thank Peter Murphy and associates (NCI, Townsville), Clive Wilkinson (AIMS, Townsville) and Cécile Debitus (ORSTOM, Noumea), for providing access to their diverse collections of marine sponges from Australia and New Caledonia; Prof. Georgy Elyakov, scientific staff and crew of the USSR RV 'Akademik Oparin' (PIBOC) for their collaborative field work at the Houtman-Abrolhos Islands (1987); Avril Ayling ('Sea Research', Daintree) for unpublished information on reproductive observations, Tony Larkum (Sydney University) for other information on several of the new species described here, and Rob Van Soest (ZMA, Amsterdam) for valuable unpublished information and comments on the manuscript. Penny Barents (AM, Sydney), Shane Parker (SAM, Adelaide), Shirley Stone (BMNH, London), Claude Lévi (MNHN, Paris), Dieter Kühlmann (ZMB, Berlin), Klaus Ruetzler (USNM, Washington) and Manfred Grasshoff (SMF, Frankfurt) are thanked for providing access to type material from their respective collections.

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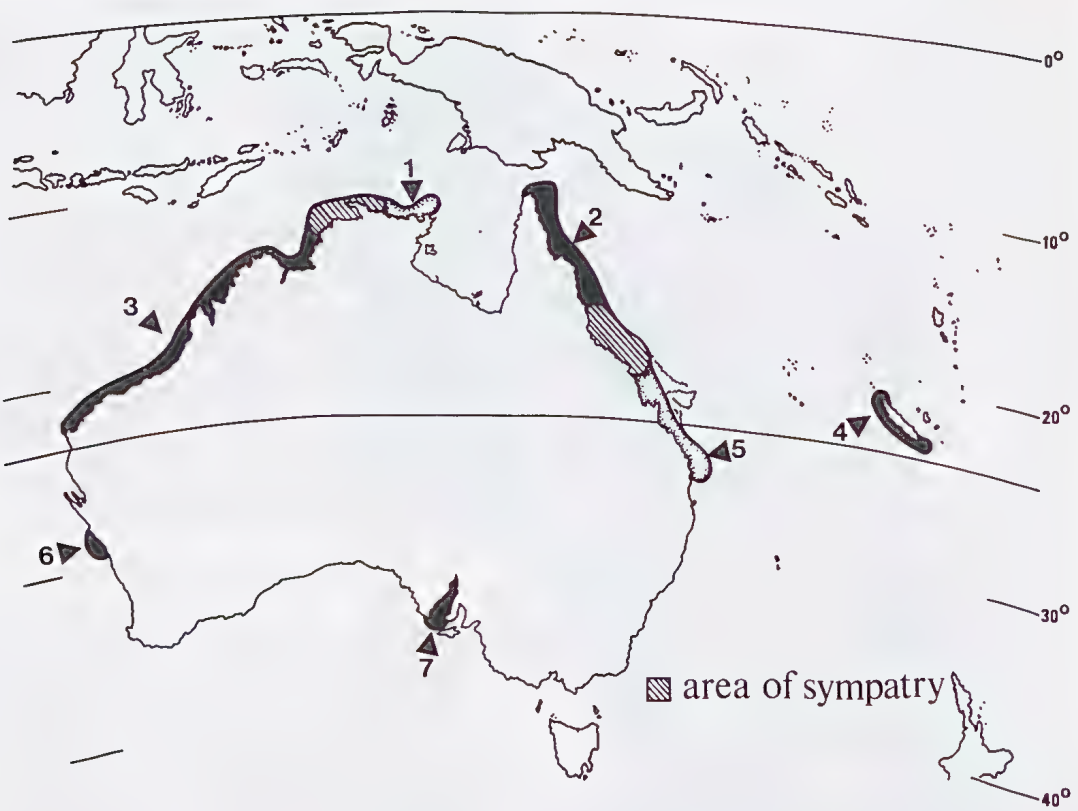

FIG. 25. Distribution of Australasian *Cymbastela* species, indicating three groups of allopatric species (numbers 4,6,7), and areas of overlap between four sympatric species (numbers 1,2,3,5) on the northeast and northwest coasts of Australia. 1, *C. stipitata*; 2, *C. coralliophila*; 3, *C. vespertina*; 4, *C. cantharella*; 5, *C. concentrica*; 6, *C. marshae*; 7, *C. notiaina*.

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THE TADPOLE OF THE AUSTRALOPAPUAN FROG *RANA DAEMELI*. *Memoirs of the Queensland Museum 32(1): 138. 1992:-* The ranid frog *Rana daemeli* (Steindachner) is widespread in New Guinea and, in Australia, occurs in northern Queensland north of Townsville (Menzies, 1987; pers. obs.).

Little is known of the biology of this species. Zweifel (1980) and Menzies (1987) analysed calls of *R. daemeli* from Papua New Guinea, and Menzies (1987) described the form of the spawn. In this note I describe the tadpole of *R. daemeli* from northern Queensland.

Tadpoles were collected with a dip net and preserved immediately in 10% formalin, or returned to the laboratory where they were kept in glass aquaria and fed fresh algae. Measurements of preserved specimens were made using a dissecting microscope with an eyepiece micrometer. All measurements are in millimetres; those involving apertures were taken from the centre of the aperture. Terminology follows Altig (1970), and the staging system is that of Gosner (1960).

Tadpoles were collected in Melaleuca swamps and temporary and permanent streams between Ollera Creek, 63km north of Townsville, and Cape Tribulation. Specimens were found primarily among debris and algae in the deepest sections of these habitats. Tadpoles and metamorphs have been collected during March, May and September, indicating that this species has an extended breeding season, or that larval development is extended.

A stage 36 tadpole is illustrated in Figure 1. Details of the oral disc are illustrated in Figure 2. A stage 36 tadpole has the following measurements: 59.6 total length, 22.0 body length, 6.4 basal tail muscle height, 5.9 basal tail muscle width, 4.0 maximum dorsal fin height located 14.8 from body terminus, 3.0 maximum ventral fin height located 16.8 from body terminus, 12.3 maximum body width, 10.2 maximum body height, 2.6 eye diameter, 7.3 interorbital distance, 3.8 internarial distance, 2.7 snout-naris, 7.0 snout-eye, 11.2 snout-spiracle, 4.2 naris-eye, 4.5 transverse oral disc diameter. Other major characteristics include; oral disc emarginate, oriented anteroventrally; marginal papillae large, in a single row laterally, two rows posteriorly, a wide gap anteriorly; papillae on posterior margin extremely elongated, forming a fringe along the posterior margin of the disc; submarginal papillae only at the corner of the jaws; spiracle short, sinistral, located ventrolaterally and oriented posterodorsally; vent tube dextral, attached to ventral fin, opening 4.0 from tail-body junction.

The tooth row formula is 2(2)/3(1). The A2 gap is wide, and the P1 gap extremely narrow. The keratinised jaw sheaths are narrow and serrated. The upper sheath is broadly curved, and the lower sheath broadly V-shaped. The eyes are dorsal. The nares are extremely small, and are covered with skin in some specimens. The fins are low, tapering to a narrow but not sharp point.

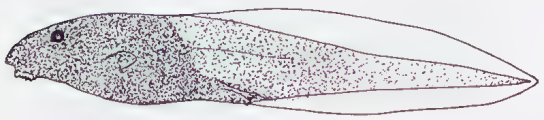

FIG. 1. Lateral view of a stage 36 *Rana daemeli* tadpole. Scale bar = 15mm.

FIG. 2. Oral disc of a stage 36 *Rana daemeli* tadpole. Scale bar = 1mm.

In life tadpoles are heavily pigmented dorsally with gold and black, with a green tinge along the midline. Black pigmentation is more prominent laterally. Tadpoles are dark grey on the anterior portion of the ventral surface, and light grey with a purple tinge on the posterior portion of the ventral surface. Small clumps of gold pigment occur on the fins. A tadpole reared to metamorphosis was olive green dorsally and grey ventrally, weighed 1.42g and was 24.3mm in length. These tadpoles belong to the Benthic (Type 2: Profundal) ecomorphological guild of Altig & Johnston (1989). The typical ranid features of an emarginate oral disc and a fringe of elongated papillae along the posterior margin of the disc (Webb & Korky, 1977) should serve to distinguish this species from other Australian tadpoles so far described.

R. Alford commented on the manuscript. Field work was funded by ARC grant A18931875 to R. Alford.

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TRACE FOSSILS FROM THE PHE FORMATION (LOWER CAMBRIAN), ZANSKAR VALLEY, NORTHWESTERN INDIA

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Hughes, N.C. & Droser, M.L. 1992 06 29: Trace fossils from the Phe Formation (Lower Cambrian), Zanskar Valley, northwestern India. *Memoirs Queensland Museum* **32**(1):139-144. Brisbane. ISSN 0079-8835.

Trace fossils from the upper part of the Tsarap Member of the Phe Formation, Zanskar Valley, northwest India, provide the first evidence for the age of these strata. *Taphrhelminthopsis* cf. *circularis* and *Helminthopsis* sp. suggest an Early Cambrian age. *T.* cf *circularis* in the absence of body fossils may indicate that these traces predate the trilobites and are correlative with the Tommotian. □ *trace fossil, Cambrian, Himalaya.*

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The lower Palaeozoic history of India is not well known, despite much recent work. The Zanskar region is particularly poorly understood, although a series of recent studies provide some understanding of the early Palaeozoic in this region (Nanda & Singh, 1976; Srikantia et al., 1980; Gaetani et al., 1986; Garzanti et al., 1986; Whittington, 1986). Trace fossils studies are currently of special significance because the Precambrian-Cambrian boundary is formally based on the appearance of key ichnogenera (Narbonne et al., 1987). This paper records trace fossils within the Phe Formation and constrains the position of the Precambrian-Cambrian boundary in this region.

TRACE FOSSILS AND THE PRECAMBRIAN-CAMBRIAN BOUNDARY IN INDIA

Following Seilacher's (1955) pioneering work on the trace fossils of the Salt Range in Pakistan recent work in India has concentrated on the use of trace fossils for recognising the Precambrian-Cambrian boundary (Tandon & Bhatia, 1978; Bhargava et al., 1982; Bhargava & Srikantia, 1982; Raina et al., 1983; Kumar et al., 1983; Shah & Sudan, 1983, 1984; Singh & Rai, 1983; Kumar et al., 1984; Kumar, 1984). The diversity of trace fossils increases at stratigraphically higher levels in pre-trilobite bearing strata of India (Tandon & Bhatia, 1978; Raina et al., 1983; Kumar, 1984), which is consistent with patterns described from many sections worldwide (e.g. Fedonkin, 1979; Crimes & Anderson, 1985; Fritz & Crimes, 1985; Crimes, 1987; Narbonne & Myrow, 1988; Narbonne et al., 1987). The Precambrian-Cambrian boundary is formally defined on the basis of trace fossils and, while initial progess has been made, much work is still needed before it can be accurately determined in the Indian Himalaya. Kumar et al. (1984, fig. 2) reported that *Phycodes* first occurs at the top of member A of the Lolab Formation in Kashmir, 750m above deposits containing Upper Riphean microflora. If complete, this section appears to be the best candidate for recognising the Precambrian-Cambrian boundary in India. A complete Precambrian-Cambrian boundary section may be present in the Krol-Tal belt, from which Ediacaran fossils (Mathur & Shanker, 1989; 1990), small shelly fossils (Bhatt et al., 1983) and archaeocyathids (Singh & Rai, 1983) have been reported. However, the Ediacaran faunas apparently occur above the small shelly fossils (Kumar, 1990), and the accuracy of some of these identifications is uncertain. M. Wade (pers. comm.) suspects that many, but not all, are algal or cyanobacterial mat structures.

STRATIGRAPHY AND TRACE FOSSILS OF THE PHE FORMATION

STRATIGRAPHY

Lowermost Palaeozoic rocks in the Zanskar Valley are assigned to three formations; the basal, silt/sandstone-dominated Phe Formation, the dolomitic Karsha formation and the silt-dominated Kargiakh Formation (Garzanti et al., 1986). Although Garzanti et al. (1986) noted bioturbation in the Phe Formation they did not recognise any fossils. Trilobite fragments have been reported (Garzanti et al., 1986) within the Karsha Formation, and late Middle Cambrian trilobites occur in the Kargiakh Formation (Garzanti et al., 1986) (some 400 m above the top of

the Phe Formation). These relationships suggest that the Phe Formation is older than late Middle Cambrian; some of the Phe Formation might be Precambrian (Garzanti et al., 1986), raising the possibility of a Precambrian-Cambrian boundary section in Zanskar.

The Phe Formation comprises at least 800 m of siltstones and fine-grained sandstone (Garzanti et al., 1986). It is divided into a silt-rich lower Tsarap Member, and an upper sandier Doda Member (Nanda & Singh, 1976). Nanda & Singh (1976) recognised an uppermost Thonde Member, from which trilobites have been collected at Kargiakh nulla (Dungrakoti et al., 1974). The trilobites were assigned to *Ptychoparia* sp and *Asaphus* sp and, on this basis, it was suggested that the Phe Formation is Upper Cambrian to Lower Ordovician (Gupta, 1978). However, further work has shown that fossiliferous strata in Kargiakh nulla are not part of the Phe Formation. Instead they overlie the Karsha Formation. These deposits are now assigned to the Surichun Member of the Kargiakh Formation (Garzanti et al., 1986). Although subsequent collection of the Kargiakh nulla site yielded neither *Ptychoparia* nor *Asaphus* (these assignments are likely incorrect), the agnostid *Lejopyge laevigata* confirms a latest Middle Cambrian age (Whittington, 1986). A variety of mid Middle Cambrian trilobites have recently been collected from the Kargiakh Formation, some from limestones, by Mr. A. Dogra and Dr. Sat Paul of Jammu University and are currently being described. As there are no major unconformities or structural discontinuities between the Kargiakh, Karsha and Phe Formations the age of the Karsha/Phe Formations is pre-mid Middle Cambrian.

Gupta & Shaw (1981) reported and figured *Ellipsocephalus hoffi* and *Agraulos* sp. which they claimed were collected from the Phe Formation in the Kargiakh and Doda valleys. Reasons to doubt the validity of this report include: 1, the grid co-ordinates given do not coincide with the positions of these localities; 2, the three dimensional, slightly distorted nature of their specimens contrasts with the condition of other Cambrian trilobites collected from the Himalaya, which are flattened and are strongly deformed; and 3, recollection of this area by M. Gaetani and N. Hughes has not revealed any fossils similar to those described by Gupta & Shaw (1981). Similar doubts about the reliability of Gupta & Shaw's (1981) paper has been recorded by Whittington (1986) and their paper should be disregarded, in line with the suggestion of Talent et al. (1990).

Trace Fossils

The Phe Formation was examined at several localities but trace fossils were observed only in the section due north of the village of Purni (33°8'24"N, 77°6'6"E) which corresponds to Section 1 on the map of Garzanti et al. (1986). These traces were described and photographed in situ and were not collected.

Within this section, traces occur in the upper part of the Tsarap Member of the Phe Formation, which is predominately composed of heterolithic dark grey siltstones and very fine grained light grey/buff sandstones. Sandstones are thinly bedded (1-5cm) and may be parallel, hummocky or cross stratified. Siltstones range from thin laminae to very thin beds (0.2-3.0cm). Where ripple structures are well preserved, wavy bedding is recognised (Fig. 1A). Wave, current, and interference ripples are all common on bedding surfaces (Fig. 1H). Short, narrow tool marks indicate palaeoflows towards the WSW. Slump features are common. The Phe Formation was deposited in an intertidal to shallow subtidal setting (Garzanti et al., 1986; pers. obs. N.C.H.).

Trace fossils are common on several bedding surfaces at the base of the section 100m north of Purni village. *Taphrhelminthopsis* cf. *circularis* (Fig. 1B-D) is most common occurring as a bilobate structure with a well defined, broad central furrow. Burrow width is 1.5-2.0cm. The furrow is about 0.2-0.3 of the width of the trace fossil. The trace fossils are sinuous to arcuate and up to 50cm long. Striations are not present. No complete circles were observed so specific assignment is questionable.

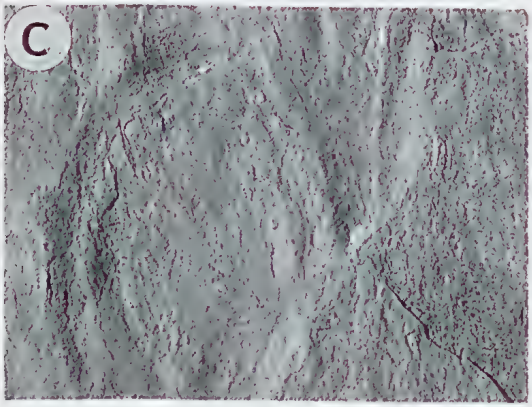
Helminthopsis (Fig. 1G) occurs as a groove, 0.2-0.4cm wide consisting of a central furrow with raised levees or as a full burrow. Traces are up to 15cm long, forming irregular meanders that were not observed to cross and commonly occur on rippled surfaces.

The tops of vertical burrows, 0.5-0.7cm in

FIG. 1. All photos except E from Upper Tsarap Member, 100 metres north of Purni, Zanskar. A, Interbedded silt and sand layers showing wavy bedding. B, *Taphrhelminthopsis* cf. *circularis* on bedding surface, ×0.2. C, *Taphrhelminthopsis* cf. *circularis* on bedding surface, ×0.5. D, detail of *Taphrhelminthopsis* cf. *circularis*, ×1. E, bedding surface showing abundant *Planolites* and other traces, scree slope between Purni and Testa, probably from Tsarap Member, ×0.3. F, back filled burrow, ×1. G, *Helminthopsis* on bedding surface, ×1. H, Bedding surfaces showing wave, current and interference ripples:

A

B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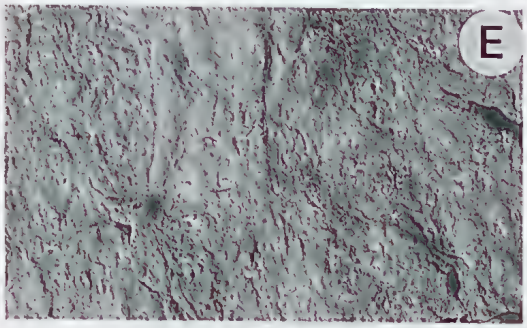
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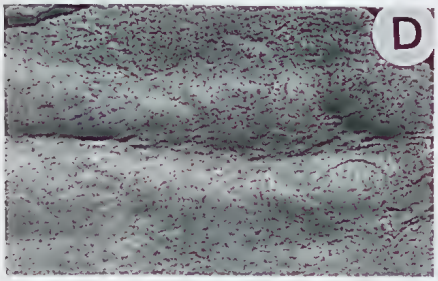
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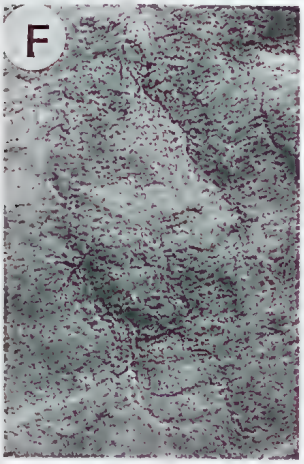
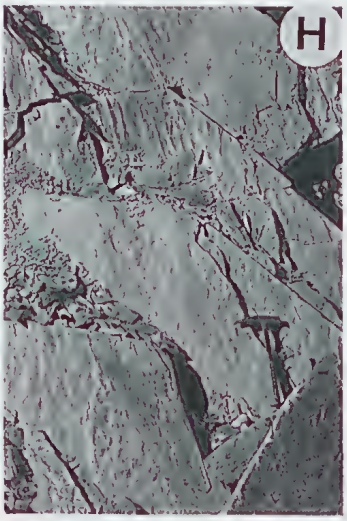

F

G


H

diameter, some apparently paired, are present on bedding surfaces, but no cross sections of these burrows were observed. Horizontal *Planolites* burrows, up to 0.8cm wide and 7.0cm long, are also present. One possible example of a back-filled burrow (Fig. 1F) occurs in siltstones. The burrow is infilled with very fine sand.

A slab of Phe Formation in scree on the track between Purni and Testa villages (Fig. 1E) shows abundant horizontal traces and vertical *Skolithos* burrows, which are 0.5cm wide and unpaired. In cross section this slab shows an ichnofabric index of 3 (Droser & Bottjer, 1986).

DISCUSSION

The trace fossils indicate that these deposits are no older than Vendian. *Taphrhelminthopsis* is characteristic of Cambrian and younger strata (Crimes, 1987, in press). Fritz & Crimes (1985) reported *Taphrhelminthopsis* from Precambrian strata from the Cassiar Mountains, British Columbia but Crimes (1987) suggested that *Taphrhelminthopsis* in these strata indicates that perhaps the boundary in this section should be lower. In the current Precambrian-Cambrian boundary stratotype in Newfoundland Taphrhelminthopsis first occurs in the second trace fossil zone, (*Rusophycus avalonensis*) above the Precambrian-Cambrian boundary (Narbonne & Myrow, 1988).

Helminthopsis similarly first appears in Cambrian strata in well documented sections (Crimes, 1987) and is also thought to be characteristic of Phanerozoic strata. Both genera occur throughout the Phanerozoic and therefore do not further constrain the age. However, *Taphrhelminthopsis circularis*, appears to range from just above the first Phanerozoic-type traces to just below the first trilobites (Crimes, 1987, in press).

Skolithos, Planolites and simple back filled burrows, all appear in the Vendian and range through the Phanerozoic and therefore do not aid in age resolution.

Crimes (1992) recognised an evolutionary development of simple sediment filled burrows from the Precambrian to the Cambrian. The straight to slightly curved *Planolites* first occurs in Vendian deposits. Slightly more complex irregularly meandering burrows which cross, such as *Gordia*, occur later in the Vendian. Burrows which spiral and have first-order meanders appear subsequently. *Helminthopsis*, which consists of irregular, but non-crossing first and second order meanders normally first occur in Cambrian strata, and are characteristic of the Early Cambrian. Crimes (1992) reported increasing complexity of 'stuffed' burrows, with the meandering bilobate stuffed burrow *Taphrhelminthopsis* characterising Early Cambrian deposits.

We suggest that at least the upper part of the Tsarap Member is of Early Cambrian age based on *Helminthopsis* and *Taphrhelminthopsis,* and particularly the close similarity to *T. circularis*. If *T. circularis* is restricted to the pre-trilobite Cambrian (Crimes, 1987), it could explain the absence of body fossils in the Phe Formation. The Precambrian-Cambrian boundary may lie within the lower, unfossiliferous 200m of the Tsarap Member of the Phe Formation.

Like most other Early Cambrian trace fossil assemblages (Crimes & Anderson, 1985; Crimes, 1987) the fossils from the Phe Formation are found in shallow, nearshore deposits. *Taphrhelminthopsis* is common in the Lower Cambrian of India, occurring in the Himalaya in southeastern Kashmir (Bhargava & Srikantia, 1982) and in the Lesser Himalaya in the Tal Formation near Kauriyala, Uttar Pradesh (Kumar et al., 1983), and possibly near Mussoorie (Singh & Rai, 1983).

ACKNOWLEDGEMENTS

Peter Jell read the manuscript and offered helpful criticisms. Mary Wade kindly discussed aspects of the paper. N.C.H. gratefully acknowledges receipt of a Natural Environmental Research Council Fellowship which enabled him to visit the Himalaya. Rae and John Sheridan provided skillful assistance in the field and excellent companionship. Rigsen Jora facilitated our travel within the region. Dawa Jora and Punzok acted as guides and we are grateful to them and to our horsemen for assisting our safe passage. Isabel Montañez and Sue Turner kindly provided essential literature.

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SCALPELLID BARNACLES (CIRRIPEDIA: THORACICA) FROM THE NORTHEASTERN AND CENTRAL EASTERN AUSTRALIAN CONTINENTAL SHELF AND SLOPE

DIANA S. JONES

Jones, D.S. 1992 06 29: Scalpellid barnacles (Cirripedia: Thoracica) from the northeastern and central eastern Australian continental shelf and slope. *Memoirs of the Queensland Museum* **32**(1): 145-178. Brisbane. ISSN 0079-8835.

Eleven species of scalpellid barnacles are described from continental shelf and slope waters off northeastern and central eastern Australia. Nine of these species were collected by the Cidaris I expedition which sampled barnacles mainly from the continental slope of north-eastern Queensland and the adjacent Coral Sea. The additional two scalpellid species were contained in the deep-water cirripede collections of the Queensland Museum, Brisbane, and the Australian Museum, Sydney. The species are fully described and illustrated since previous descriptions often have described conchology only and detailed descriptions, especially of arthropodal structures and of dwarf or complemental males, are either absent or are brief and inadequate. All the scalpellids collected by Cidaris I were first records from Queensland waters and, with the exceptions of *Verum australicum* Hoek and *Anguloscalpellum pedunculatum* (Hoek), first records from Australian waters. They were listed, but not described, in the recent catalogue of the Australian cirripede fauna (Jones et al., 1990). In the present contribution *Trianguloscalpellum hirsutum* sensu Jones et al. (1990) is regarded as a synonym of *T. hamulus* (Hoek), *T. hamulus* and *A. persona* are new records for Australian seas, and *S. stearnsii* is recorded from Queensland for the first time. ☐ *Crustacea, Thoracica, Lepadomorpha, Scalpellidae, Australia, new records, taxonomy.*

Diana S. Jones, Western Australian Museum, Francis St, Perth, Western Australia 6000, Australia; 14 November, 1991.

Documentation of the littoral and shallow water cirripede fauna of Australia began during the French expeditions of discovery at the beginning of the nineteenth century (Jones, 1991). The first contributions towards knowledge of the deeper water Australian cirripede faunas were not made until the late nineteenth and early twentieth centuries and are contained in Hoek's reports on the Cirripedia collected during the voyages of 'Challenger', between 1873 and 1876, and 'Siboga', from 1899 to 1900 (Hoek, 1883, 1907, 1913). Subsequently significant contributions have been made through the works of Calman (1918, 1919), Nilsson-Cantell (1927, 1928), Newman (1960), Utinomi (1968), Foster (1981) and Zevina (1981a). More recently, documentation of Australian shelf and slope (as well as littoral) cirripede faunas has been completed (Jones et al., 1990).

The Cidaris I expedition, which sampled the deep-sea fauna of the Coral Sea, was organised by the James Cook University of North Queensland, Townsville, in 1986. Some samples were obtained from the continental shelf and the majority from the continental slope and adjacent Coral Sea off the northeastern Queensland coast, out from Townsville (19°16'S, 146°49'E), at depths of 287 to 1612m. The present report covers the nine species of scalpellid barnacles collected by this expedition and further reports will cover the remaining lepadomorphs and the Verrucomorpha and Balanomorpha collected during the expedition. On examination of the deep-water barnacle collections housed in the Queensland Museum, Brisbane, and the Australian Museum, Sydney, two further scalpellid species were discovered that had been collected from the waters of the north-eastern and central eastern Australian continental slope. For comparative purposes, slope material from northwestern Australia housed in the Western Australian Museum, Perth, was utilized to validate identifications. Where relevant this material has also been included in the present contribution.

Eleven continental shelf and slope scalpellids are described and illustrated. Supplementary descriptions of each species, especially of arthropodal structures and dwarf and complemental males, are given since these have either not been described previously, or existing descriptions are brief or inadequate. The classification and sequence used for the Scalpellidae is that of Zevina (1981a, 1982). All measurements are in centimetres.

Abbreviations: AM, Australian Museum, Sydney; QM, Queensland Museum, Brisbane; WAM, Western Australian Museum, Perth; CH, capitular height; CW, capitular width; PL, peduncular length; PW, peduncular width; R, range; (R) right; (L) left. Registration numbers of AM material are prefixed by P, QM material by W (with Cidaris I material indicated by W*) and WAM material by WAM.

LIST OF THE SPECIES

1. *Scalpellum stearnsii* Pilsbry,1890
*2. *Alcockianum alcockianum* (Annandale,1905)
3. *Alcockianum persona* (Annandale,1916)
*4. *Annandaleum lambda* (Annandale,1910)
*5. *Verum australicum* (Hoek, 1883)
*6. *Anguloscalpellum pedunculatum* (Hoek, 1883)
*7. *Amigdoscalpellum daschae* Zevina,1981
*8. *Amigdoscalpellum elegans* (Hoek,1907)
*9. *Trianguloscalpellum hamulus* (Hoek,1907)
*10. *Arcoscalpellum michelottianum* (Seguenza,1876)
*11. *Arcoscalpellum moluccanum* (Hoek,1883)

*indicates material collected by Cidaris I.

Trianguloscalpellum hirsutum sensu Jones et al. (1990) is regarded as a synonym of *T. hamulus* (Hoek, 1907), *T. hamulus* and *A. persona* are new records from Australian seas, and *S. stearnsii* is recorded from Queensland waters for the first time.

SYSTEMATICS

Order THORACICA Darwin, 1854
Family SCALPELLIDAE Pilsbry, 1916
SCALPELLINAE Pilsbry, 1907
Scalpellum Leach, 1817

Scalpellum stearnsii Pilsbry, 1890
(Figs 1, 2)

Scalpellum magnum Darwin, 1851: 18, pl. 1, fig. 1.
Scalpellum stearnsi(i) Pilsbry, 1890a: 96; Pilsbry, 1890b: 441, fig.; Weltner, 1897: 250; Gruvel, 1905: 44, fig. 46; Pilsbry, 1907: 14, pl. 4, figs 1-5; Krüger, 1911: 18, figs 26-35, pl. 2, figs 18-19; Pilsbry, 1911: 61; Annandale, 1916b: 293; Broch, 1922: 235, fig. 6; Broch, 1931: 16; Hiro, 1933: 22, fig. 4, pl. 1 figs 5-5a; Nilsson-Cantell, 1933: 33; Newman & Ross, 1971: 123; Zevina 1981a: 98, fig. 68; Rosell, 1981: 279, pl. 1e; Ren, 1987: 189, fig. 1:1.
Scalpellum calcariferum Fischer, 1891: 116, fig.
Scalpellum inerme Annandale, 1905: 75, fig. 1, pl. 8, figs 1-1a; 1909: 270; Pilsbry, 1907: 14.
Scalpellum stearnsii var. *inerme*: Annandale, 1916b: 293; Nilsson-Cantell, 1928: 2, fig. 1; Broch, 1931: 17; Nilsson-Cantell, 1933: 33; 1934: 44, pl. 5 fig. 1.
Scalpellum stearnsii var. *robusta* and var. *gemina* Hoek, 1907: 69, 70, pl. 6, figs 1-12; Pilsbry, 1911: 62; Weltner, 1922: 16.
Scalpellum stearnsii inerme: Nilsson-Cantell, 1938: 8; Newman & Ross, 1971: 123.

TYPE LOCALITY
East coast of Japan, between the bay of Tokyo and the Inland Sea.

DISTRIBUTION
Indian Ocean, Malay Arch., Indonesia, northwestern Australia, South China Sea, Japan. Depth range 182-2117m. Now known from central eastern Australia (465-562m).

MATERIAL EXAMINED
W15533, S of Swain Reefs (23°28'S, 153°19'E), 562m, 1 spec.; W10196, 130km E of Capricorn Gp (23°28'S, 153°19'E), 562m, 15 specs; W1097, 100km E of Capricorn Gp (23°30'S, 153°04'E), 540m, 6 specs; W11303 (part), E of Bunker Gp (23°54'S, 153°01'E), 465m, 1 spec.; W14339 (27°20'S, 153°53'E), 600m, 1 spec.; P35288, E of Gold Coast (28°02'-27°59'S, 153°59'E), 540m, 1 spec.

DESCRIPTION
Large individuals female. Capitulum laterally compressed, fourteen capitular plates, calcareous, partially reduced. Carina angularly flexed, umbo at angle. Carinolatus with horn-like projection which is very variable, almost wanting to strongly developed, when free projecting portion can be one-third to one- half length of plate. Peduncle with prominent external rings of overlapping calcareous scales. Measurements of the 25 specimens: CH 1.75-4.93 (mean 3.28), CW 1.05-3.90 (mean 2.17), PL 1.43-12.85 (mean 4.23), PW 0.55-1.98 (mean 23).

Cirrus I with rami very unequal in length and shape, anterior ramus much shorter than posterior ramus, proximal and intermediate segments of anterior ramus very protuberant especially towards posterior, segments transversely oblong and only united with one another over part of breadth, segments of posterior ramus square. Cirri II and III elongated, rami subequal, bearing three to six pairs of long setae on anterior margins, anterior ramus of cirrus II more setose than

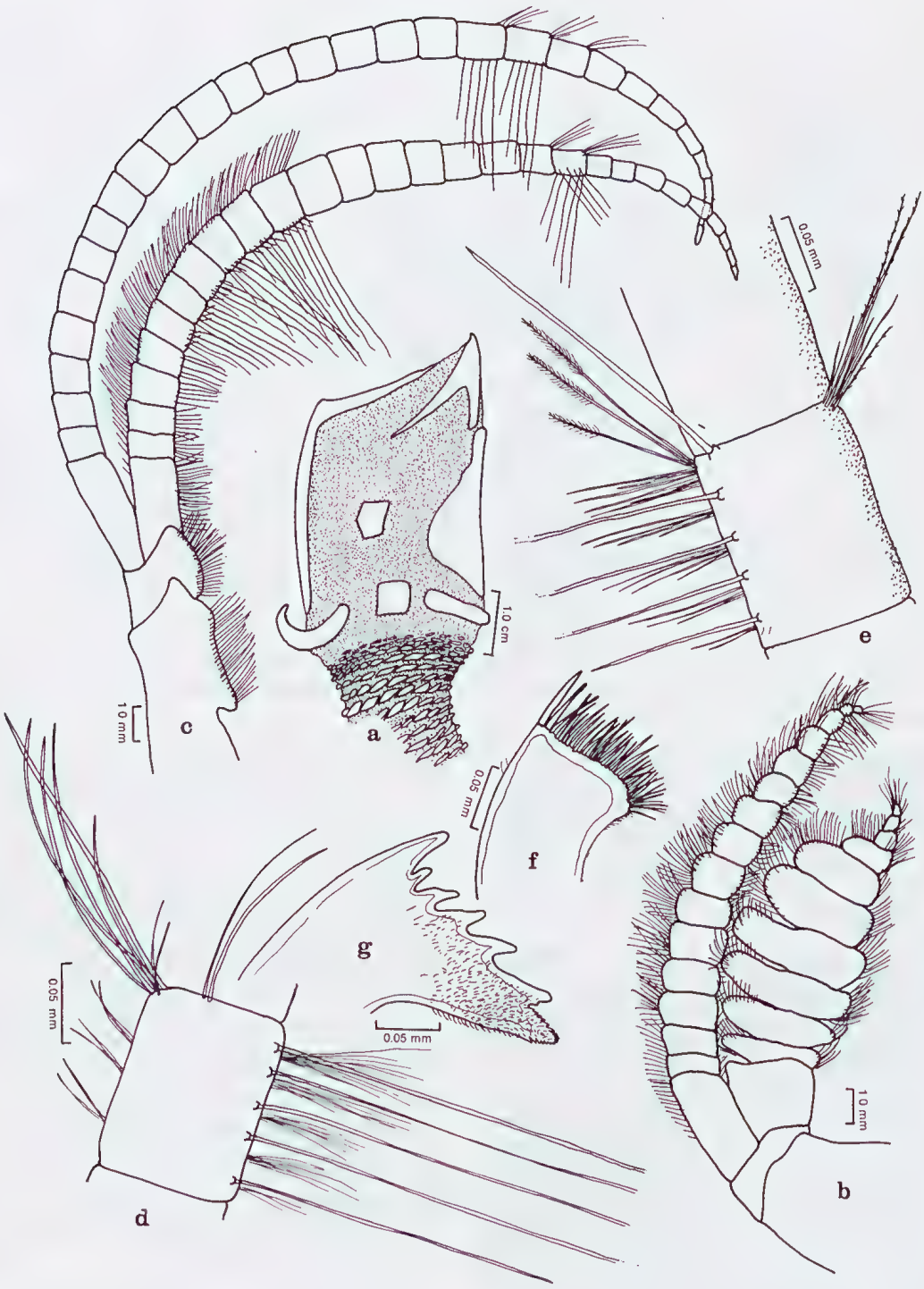

FIG. 1. *Scalpellum stearnsii* Pilsbry, 1890. a, lateral view. b, cirrus I. c, cirrus II. d, intermediate segments, anterior ramus, cirrus III. e, intermediate segments, anterior ramus, cirrus V. f, maxillule. g, mandible.

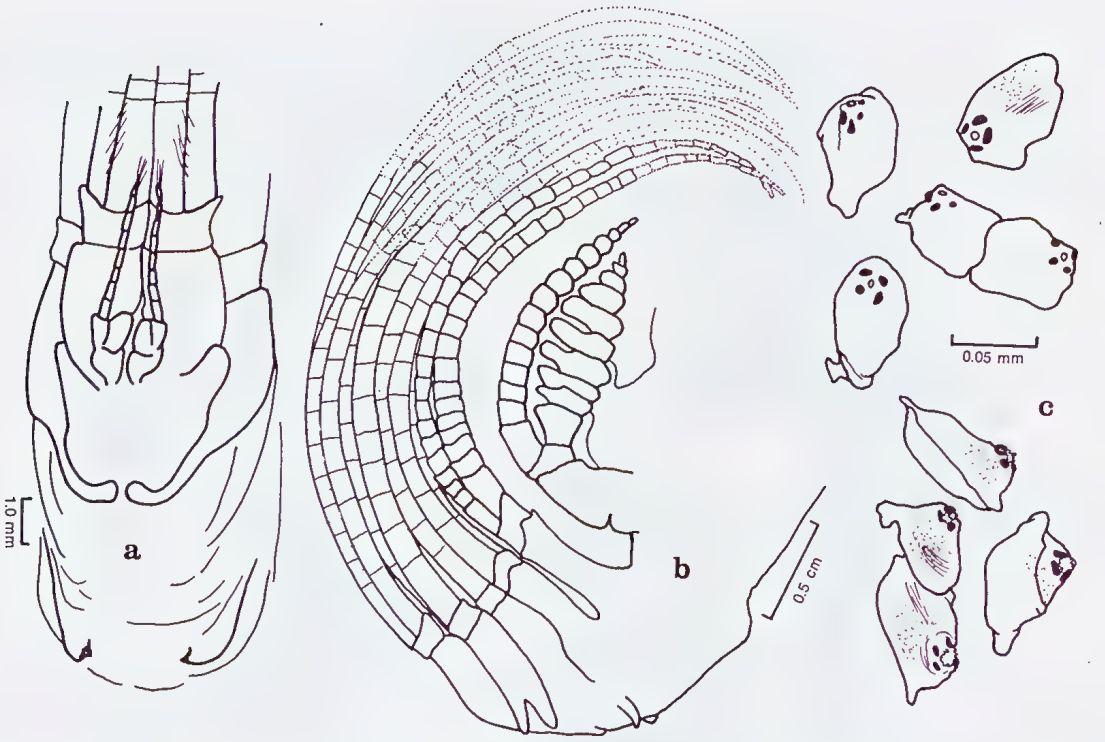

FIG. 2. *Scalpellum stearnsii* Pilsbry, 1890. a, posterior view, caudal appendages and pedicels of posterior cirri. b, lateral view of prosoma. c, dwarf males.

posterior ramus of cirrus II and both rami of cirrus III. Cirri IV, V and VI very long, rami subequal, segments elongated, bearing five to seven pairs long setae on anterior margins, posterior margins of proximal segments of cirri V and VI bearing dense scales, scales more numerous on anterior rami. Chaetotaxy ctenopod. Cirral formulae, see Table 1.

Maxillule with sinuous cutting edge bearing many setae (28-34 pairs), seta at upper angle stout and slightly larger than remainder. Mandible with five main teeth, simple, second smallest, subsidiary teeth may be present between main teeth, lower angle pectinate with short, chitinous hairs. Labrum strongly bullate, not cleft, teeth absent. Caudal appendages small, multi-articulate (6-10 segments), slightly longer than height of pedicel of cirrus VI, with tuft of long setae apically.

Dwarf males (8-10) at occludent margins of both scuta of female, located just above adductor muscle in deep pits in scutal membrane; sac-like, boat-shaped when viewed laterally, peduncle and capitulum not differentiated, four rudimentary, calcareous plates around subterminal orifice, short rudimentary tentacles between plates, body externally covered with minute erect spicules, two small, prehensile antennae on ventral surface.

REMARKS

The species has been reported from northwestern Australian waters (Jones et al., 1990) but not previously from eastern Australia. S. *stearnsii* is similar to *S. scalpellum* (Linnaeus) (= *S. vulgare* Leach) but the form of the carinolatera distinguishes *S. stearnsii*.

The species was first described from shallow water (11-18m), from the east coast of Japan (Pilsbry, 1890a,b). One year later Fischer (1891) described *S. calcariferum* from Sagami Bay, Japan, which later authors considered to be synonymous with *S. stearnsii* Pilsbry (Weltner, 1897; Gruvel, 1902). Fischer (1891) and Annandale (1909) also both pointed out the close resemblance between *S. stearnsii* Pilsbry and the fossil species *S. magnum* Darwin of the Coralline Crag, Sudbourne.

S. inerme, a species with highly degenerate capitular plates, was described from a depth of 293m from the Bali Straits (Annandale, 1905). Pilsbry (1907) considered *S. inerme* a distinct

TABLE 1. Measurements and cirral formulae of *Scalpellum stearnsii* Pilsbry, 1890.

CH	CW	PL	PW		CI	CII	CIII	CIV	CV	CVI	Ca
3.72	2.35	5.59	1.18	(R)	11/17	25/28	31/32	30/30	30/30	33/33	8
3.98	4.64	5.35	1.50	(R)	11/15	30/30	33/24+	28+/25+	33+/28+	27+/28+	10
4.76	3.08	6.87	1.70	(R)	11/16	29/29	35/24	36/34	37/35	36/35	10

species. Hoek (1907) established *S. stearnsii* var. *gemina*, which also had degenerate plates, and var. *robusta* which had a broader and longer capitulum than the typical form, from specimens collected by 'Siboga' in the Malay Archipelago at depths of 204-450 m. Pilsbry (1911) synonymized *S. stearnsii* var. *gemina* with *S. inerme*, but considered var. *robusta* identical with the typical form. However, Annandale (1916b), after examining a good series of specimens from Japan and the Malay Archipelago, considered *S. inerme* to be an extreme form of Hoek's var. *gemina* and proposed the degenerate plate form as *S. stearnsii* var. *inerme*, a view with which Nilsson- Cantell (1928, 1934) agreed. Annandale (1916b) found two Japanese specimens referable to var. *robusta*, and a number of indeterminate forms between var. *robusta* and var. *gemina*, and suggested that, as there was no evidence for Japanese and Malayan races, the two varieties should be united under *S. stearnsii*.

The specimens listed here represent the first records of *S. stearnsii* from eastern Australian waters. The specimens showed conchological characters which have been ascribed to the degenerate plate forms *S. stearnsii* var. *gemina* and *S. inerme* (tergum incompletly calcified in the form of an inverted V, scutum and upper latus reduced in size, peduncular scales smaller, arranged in more numerous rows). Soft-parts morphology and the structure of the dwarf males, however, agreed with descriptions of the more perfectly calcified form *S. stearnsii*, thus supporting the inclusion of *S. inerme* and *S. stearnsii* var. *gemina* in synonymy with the typical form.

MEROSCALPELLINAE Zevina, 1978
Alcockianum Zevina 1978

Alcockianum alcockianum (Annandale, 1905) (Fig. 3)

Scalpellum alcockianum Annandale, 1905: 82; 1906a: 392; 1906b: 138; 1907: pl. 1, fig. 2, pl. 2, figs 2-2b; 1913: 228, 229; 1916a: 129, pl 6 fig. 5.

Scalpellum (Scalpellum) alcockianum: Calman, 1918: 115; Nilsson-Cantell, 1928: 6, fig. 3; 1931: 2; 1938: 7.

Arcoscalpellum alcockianum: Newman & Ross, 1971: 60; Lakshmana Rao & Newman, 1972: 70.

Alcockianum alcockianum: Zevina, 1978b: 1345; 1981a: 149, fig. 106.

TYPE LOCALITY

S of Ceylon (5°48'15"N, 80°56'E); 'Investigator' station 277; 1750-1609m.

DISTRIBUTION

Indian Ocean, Malay Arch., Indonesia, between Java and Australia (10°45'S, 120°50'E), between southeastern Austalia and New Zealand (37°00'S, 165°00'E), New Zealand (46°16'S, 173°22'E), mid-Pacific Ocean (18°31'N, 179°36'W). Depth range 945-1800m. Now also recorded from northeastern and central eastern Australian waters (945-1950m).

MATERIAL EXAMINED

W*13256 (16°54'S, 147°14'E), 1473-1590m, 3 specs; P35286 E of Orient Pt, (34°56'-54'S, 151°15'-17'E), 1098- 1134m, 3 specs; P35287 E of Shoalhaven Heads, (34°53-50'S, 151°14'-15'E), 945-1017m, 1 spec.; P35294 E of Long Reef Pt, (33°43'-40'S, 152°03'-05'E), 1026-1053m, 3 specs.

SUPPLEMENTARY DESCRIPTION

Large individuals hermaphrodite. Capitulum oval, inflated in upper half, especially between tergum and neighbouring valves. Fourteen capitular plates, concealed by and embedded in thick, opaque membrane, externally velvety; some capitular plates imperfectly calcified, widely separated, paired plates relatively small. Peduncle variable in length, depending on degree of contraction, calcareous scales transversely elongated, arranged in alternating rows. Measurements of the 10 specimens: CH 3.15- 6.60 (mean 5.28), CW 2.47-5.81 (mean 4.31), PL 2.41-8.65 (mean 4.82), PW 1.14-2.90 (mean 2.36).

Cirrus I setose, well separated from cirrus II, anterior ramus shorter than posterior ramus, proximal segments of anterior ramus protuberant posteriorly, inner surfaces of segments of both

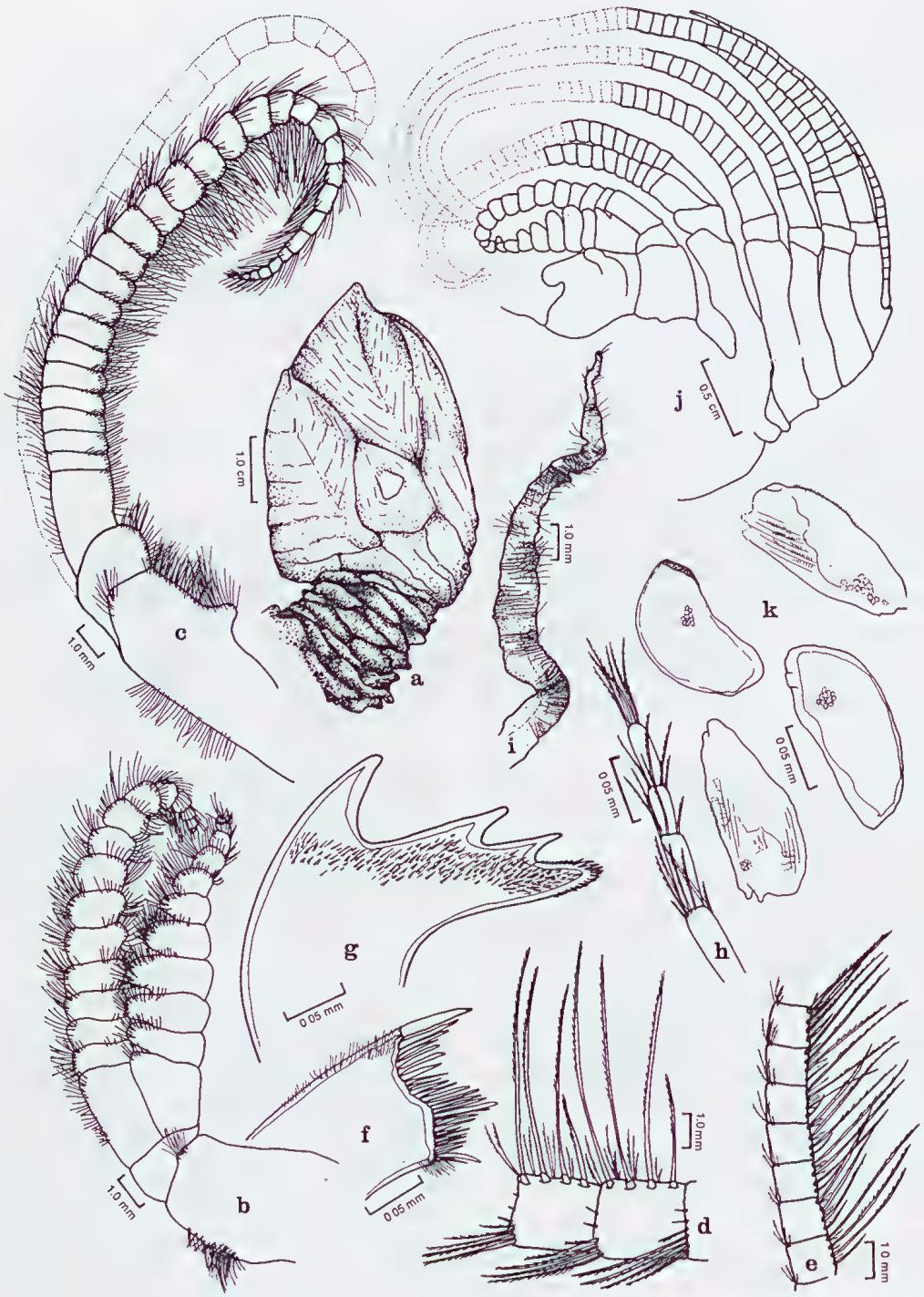

FIG. 3. *Alcockianum alcockianum* (Annandale, 1905). a, lateral view. b, cirrus I. c, cirrus II. d, distal segments, posterior ramus, cirrus II. e, intermediate segments, anterior ramus, cirrus V. f, maxillule. g, mandible. h, distal tip of caudal appendage. i, penis. j, lateral view of prosoma. k, complemental males.

TABLE 2. Measurements and cirral formulae of *Alcockianum alcockianum* (Annandale, 1905)

CH	CW	PL	PW		CI	CII	CIII	CIV	CV	CVI	Ca
3.55	4.10	2.55	2.12	(R)	11/15	26/29	36/36	40/38	39/40	42/40	28
4.84	3.26	2.41	1.80	(R)	11/16	28/31	36/36	41/41	45/44	42/39	29
5.79	4.10	2.55	2.12	(R)	9/16	29/27	34/37	37/36	42/44	41/42	27

rami extremely setose. Cirrus II long, rami subequal, anterior ramus more densely setose than posterior ramus, setae setulate, inner surfaces of segments of both rami densely setose. Cirri III to VI very long, cirri increasing in length towards posterior, rami subequal, segments elongate bearing three to five pairs long, setulate setae on anterior faces, bunch of long finely setulate setae at postero-distal corner of proximal segments of cirri III to V. Chaetotaxy ctenopod. Cirral formulae, see Table 2.

Maxillule with sinuous cutting edge bearing numerous paired setae (30-38 pairs), stout spine at upper angle. Mandible with three main teeth, first large, acute, widely separated from rest, lower angle pectinate. Labrum prominent, bullate. Caudal appendages multi-articulate (22-30 segments), one-third to one-half length of cirrus VI, distal borders of segments with circlets of setae bearing fine setules, terminal segment with dense tuft of long setae with fine setules. Penis one-quarter length of cirrus VI, slender, minutely annulated, tapering distally, sparsely setose, setae long, plumose. Complemental males (3-4) at occludent margins of both scuta of hermaphrodite, located just above adductor muscle, in shallow pocket formed by fold in scutal membrane; sac-like, ovoid, calcareous plates and cirri absent, orifice slit-like, lateral; externally with elongated spicules arranged in transverse rows.

Remarks

Material collected by Cidaris I is the first record of *A. alcockianum* within Australian waters (Jones et al., 1990). Additional material examined in the course of this study has extended the range of the species from northeastern to central eastern Australia. The specimens agreed in general with published descriptions for this species. Some variation in the form of the tergum has been described - for example, the scutal margin of the tergum may be less hollowed out (Annandale, 1906a; Nilsson-Cantell, 1928) or more hollowed out (Annandale, 1916a; Lakshmana Rao & Newman, 1972). The Australian series (n = 10) demonstrated ontogenetic changes of this plate, which is less hollowed out in smaller specimens (e.g. CH 3.55) but more hollowed out as capitular size increases (e.g. CH 6.60).

Nilsson-Cantell (1928) described a female specimen of *A. alcockianum* from Mozambique Channel at a depth of 1647m. All other descriptions of this species are based on hermaphrodites, including the Australian series.

Alcockianum persona (Annandale, 1916) (Figs 4,5)

Scalpellum persona Annandale, 1916b: 295, pl. 4, fig. 3, pl. 5, figs 7-8, pl. 6, figs 3-5; Calman, 1918: 120; Nilsson-Cantell, 1934: 44, pl. 5, fig. 2.

Alcockianum persona: Zevina, 1978b: 1345; 1981a: 150, fig. 107.

Graviscalpellum persona: Foster, 1980: 527, fig. 1e, 2.

Type Locality

Timor Sea (10°22'30"S, 120°7'30"E); 109-366m; bottom temp 13.1°C.

Distribution

Indonesian seas, also New Zealand. Depth range 109-915m. Now also recorded from eastern Australia (550m).

Material Examined

W11327, E Bunker Gp (23°15'S, 153°07'E), 550 m, 7 specs.

Supplementary Description

Large individuals hermaphrodite. Capitulum ovoid, inflated. Fourteen capitular plates embedded and mostly concealed by opaque, thick membrane, externally finely hirsute; umbos apical, apices projecting through membrance (especially carinolatera); some capitular plates imperfectly calcified (e.g. terga), all plates except scuta relatively small, especially inframedian latus. Peduncle as long as or longer than capitulum, narrowing towards capitular junction, large calcareous scales transversely elongated, arranged in alternating rows. Measurements of the 7 specimens: CH 1.55-4.05 (mean 3.20), CW 1.02-2.79 (mean 2.07), PL 1.62-5.33 (mean 3.40), PW 0.63-1.86 (mean 2.31).

FIG. 4. *Alcockianum persona* (Annandale, 1916). a, lateral view. b, cirrus I. c, cirrus II. d, intermediate segments, anterior ramus, cirrus III. e, intermediate segments, anterior ramus, cirrus V. f, maxillule. g, mandible.

Cirrus I setose, set higher than and slightly separate from cirri II to VI, anterior ramus shorter than posterior ramus, proximal and intermediate segments of anterior ramus protuberant especially towards posterior, inner surfaces of segments of both rami with dense, setulate setae. Cirrus II long,

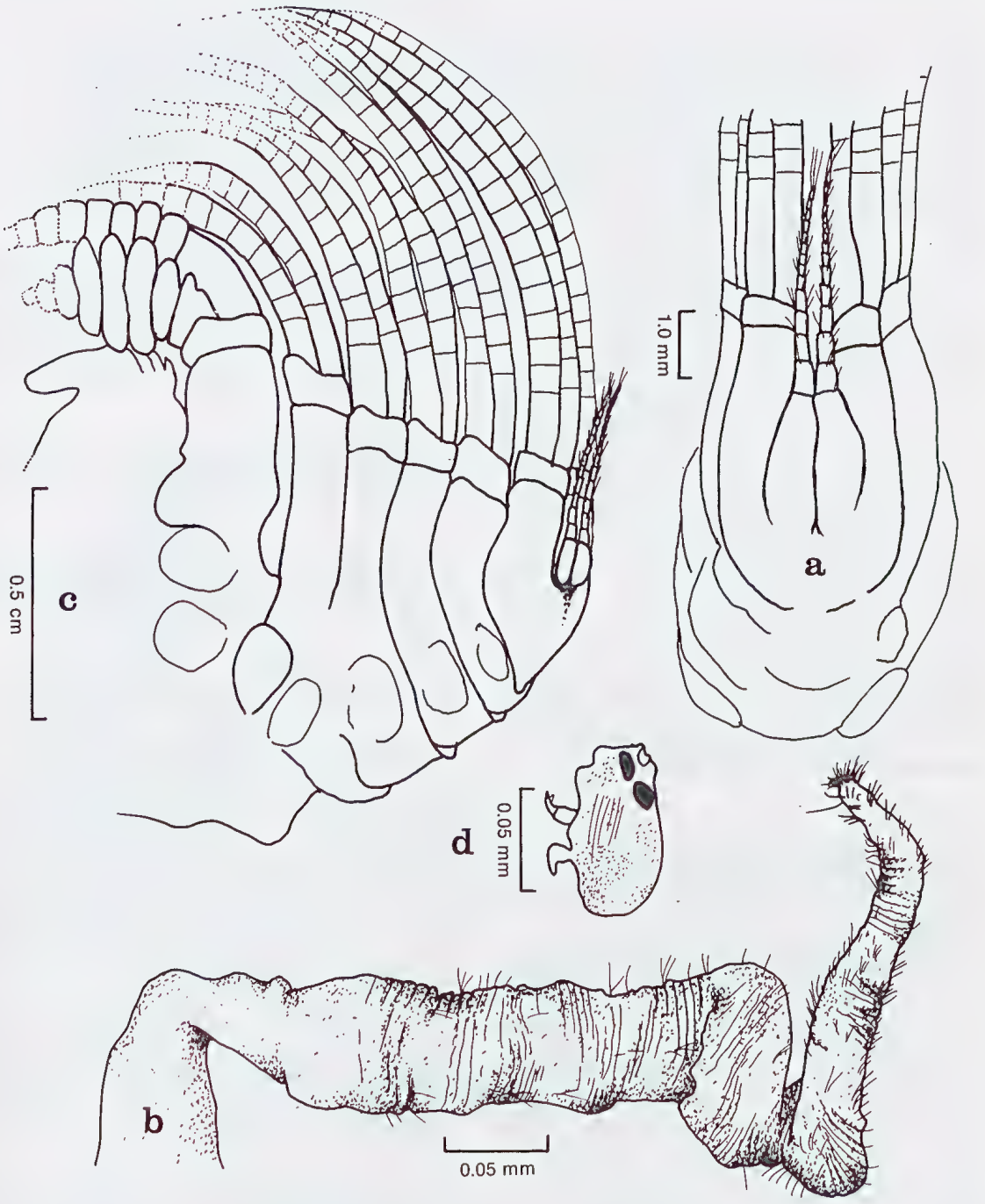

FIG. 5. *Alcockianum persona* (Annandale, 1916). a, posterior view, caudal appendages and pedicels of posterior cirri. b, penis. c, lateral view of prosoma. d, complemental male.

TABLE 3. Measurements and cirral formula of *Alcockianum persona* (Annandale, 1916).

CH	CW	PL	PW		CI	CII	CIII	CIV	CV	CVI	Ca
4.05	2.79	4.40	1.86	(R)	14/18	26/28	36/38	17+/17+	15+/14+	15+/17+	13

rami subequal, anterior ramus more setose than posterior ramus, setae setulate. Cirri III to VI very long, cirri increasing in length towards posterior, rami subequal, segments square to elongate, bearing three to six pairs long setulate setae on anterior faces, bunch of long, finely setulate setae at postero-distal corner of proximal segments of cirri III to VI. Chaetotaxy ctenopod. Cirral formula, see Table 3.

Maxilla with characteristic development of olfactory organ in the form of a blunt process. Maxillule with slightly sinuous cutting edge bearing numerous paired setae (25-30 pairs), two stout spines at upper angle. Mandible with 5 teeth, first acute, large, widely separated from remainder, lower angle molariform. Labrum extremely bullate, prominent. Caudal appendages multiarticulate (13-16 segments), twice length of pedicel of cirrus VI, segments with circlets of setulate setae, distal segment with dense tuft of setae, proximal segment expanded. Penis relatively long, one-third to one-half length of cirrus VI, annulated, tapering distally, setose towards apex, apex blunt with circlet of fine short setae. Complemental males at occludent margin of both scuta of hermaphrodite, located just above adductor muscle in deep pit in scutal membrane; ovoid, sac-like, four reduced calcareous plates around subterminal orifice, externally with small spicules, two prehensile antennae on ventral margin.

REMARKS

A. persona is similar to *A. alcockianum* but the two species are easily distinguished by characters of the tergum, carinolatera, caudal appendages and mandible.

The specimens of *A. persona* described above are the first collected from Australian seas. These specimens agree in general with published descriptions of conchology for *A. persona* (Annandale, 1916). However, the form of the mandible of Australian specimens differs from that previously described in that they exhibit five definite teeth, rather than four as figured by Annandale (1916b) for Indonesian material and Foster (1980) for New Zealand specimens. Australian specimens also do not exhibit a notch on the maxillule, whereas New Zealand specimens show a slight notch (Foster, 1980) and Indonesian material a broad shallow notch (Annandale, 1916b). The characteristic blunt conical olfactory lobe of the maxilla is, however, exhibited by Indonesian, Australian and New Zealand specimens.

Annandaleum Newman & Ross, 1971

Annandaleum lambda (Annandale, 1910) (Fig. 6)

Scalpellum lambda Annandale, 1910: 115; 1913: 234; 1916a: 130, pl.7, figs 6, 6a, pl. 8, figs 12-15.
Scalpellum longius Annandale, 1913: 234; 1916a: 130, pl. 7, figs 5, 5a; Stubbings, 1936: 27, fig. 11.
Annandaleum lambda: Newman & Ross, 1971: 122; Zevina, 1981a: 168, fig. 120.

TYPE LOCALITY

Eastern Indian Ocean (13°54'15"N, 94°02'15"E); 'Investigator' station 372; 1176m.

DISTRIBUTION

Indian Ocean. Depth range 237-1960m. Now also recorded from northeastern Australia (956-969m).

MATERIAL EXAMINED

W*13238 (18°08'S, 147°36'E), 956-969m, 1 spec.

SUPPLEMENTARY DESCRIPTION

Large individuals female. Capitulum irregularly ovate, laterally compressed. Fourteen capitular plates, smooth, thin, imperfectly calcified, separate, eight in shape of Greek lambda (λ). Inframedian latus large, vase-shaped. Peduncle shorter than capitulum, numerous calcareous scales present, narrow, transversely elongated, arranged in alternating rows. Cirrus I long, placed at a distance from cirrus II, rami very unequal, anterior ramus shorter and broader than posterior ramus; inner surfaces of both rami densely setose. Cirri II to VI very long, cirri increasing in length to posterior, rami subequal, segments elongate, bearing four to six pairs of long setae on anterior faces. Chaetotaxy ctenopod. Cirral formula, see Table 4.

Maxillule with definite notch, cutting edge below notch bearing two to three pairs setae, lower angle spinose, three stout subequal spines at upper angle. Mandible with three main teeth, lower angle pectinate. Labrum bullate. Caudal append-

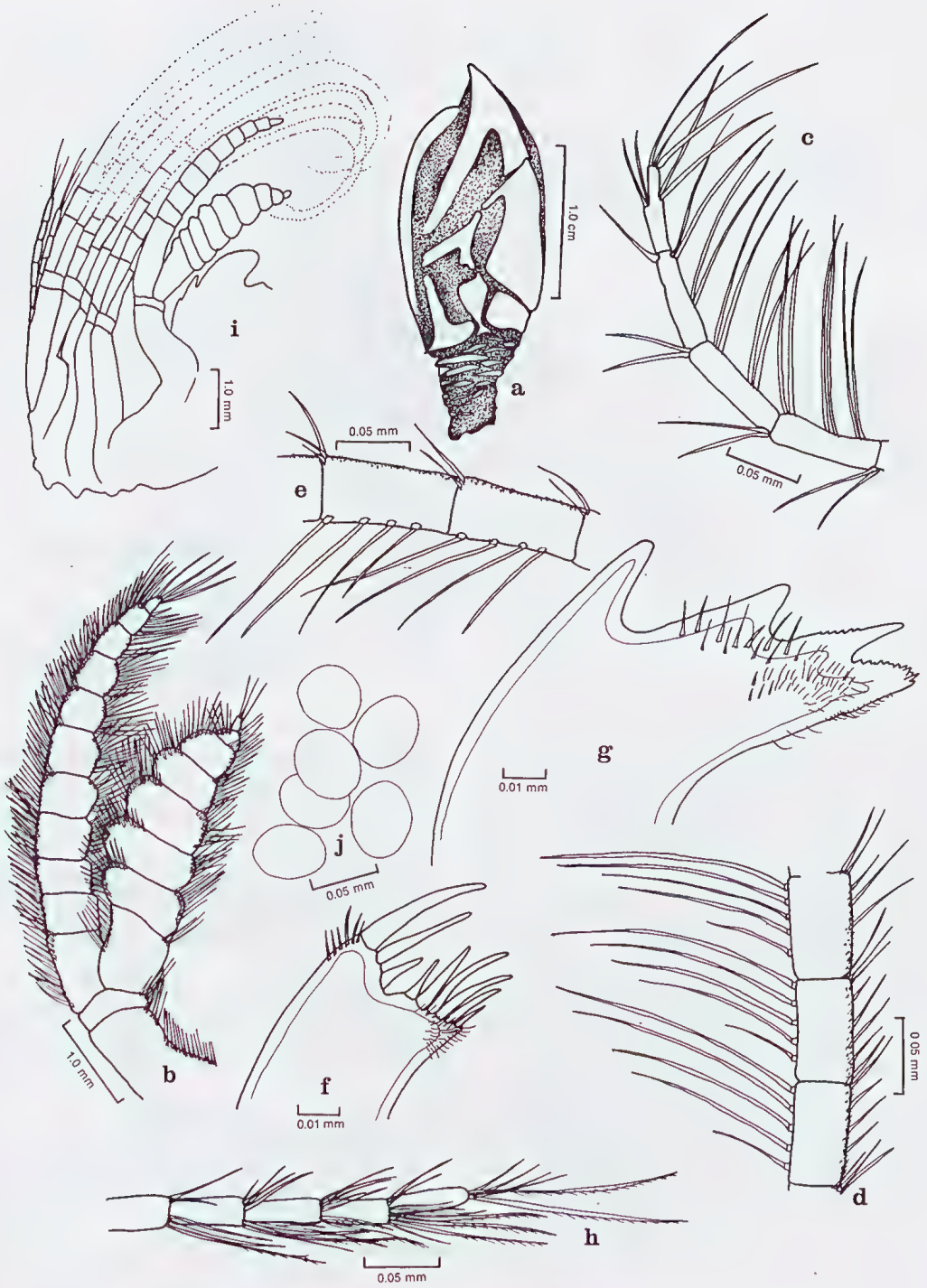

FIG. 6. *Annandaleum lambda* (Annandale, 1910). a, lateral view. b, cirrus I. c, distal segments, posterior ramus, cirrus III. d, intermediate segments, anterior ramus, cirrus III. e, intermediate segments, anterior ramus, cirrus V. f, maxillule. g, mandible. h, distal tip of caudal appendage. i, lateral view of prosoma. j, ova.

TABLE 4. Measurements and cirral formula of *Annandaleum lambda* (Annandale, 1910).

CH	CW	PL	PW		CI	CII	CIII	CIV	CV	CVI	Ca
1.68	0.94	0.60	0.61	(R)	$\frac{8}{12}$	$\frac{18}{18}$	$\frac{21}{23}$	$\frac{23}{25}$	$\frac{26}{27}$	$\frac{29}{29}$	8

ages moderately long, one-fifth length of cirrus VI, multi-articulate (6-8 segments), long setae with setules at distal tip. Penis absent. Dwarf males unknown. Ova large, ovoid, yolky, lemon yellow in preserved material.

Remarks

This species was first described by Annandale (1910) from material collected in the Andaman Sea. Annandale (1913) also described *S. longius* from the Andamans and commented that the species may possibly be '... merely a complete form of *S. lambda*...', differences being the degree of reduction of the capitular plates, the structure of the carinolatera and the relative lengths of the rami of cirrus I and the number of segments in the caudal appendages. Stubbings (1936) examined *S. longius* from Zanzibar and found the specimens agreed with the type description and '...showed no tendency to vary towards *S. lambda*'.

The sole Australian specimen described here shows characters attributable to both *S. lambda* and *S. longius*. The form of the carinolatera and the degree of reduction of the capitular plates agree in general with conchology described for *S. lambda* but differ in the following details: the apex of the carina almost touches the carinal margins of the terga; the tergal branch of the scutum is much shorter than that illustrated by Annandale (1910) but not as short as shown by Zevina (1981a); scutum, rostrolatera and carinolatera are more similar to the form illustrated by Annandale (1910) than that of Zevina (1981a); scutal arm of upper latus exhibits a bifid tip. Mandibles and maxillules of the Australian material resemble the forms figured by Stubbings (1936) for *S. longius*. In addition, both mandibles of the Australian specimen have three small, well- spaced spines on the upper margin of the third tooth and on the upper margin of the lower angle, which have not been figured previously for either *S. lambda* or *S. longius*. Rami of cirrus I in the Australian specimen are very unequal in length. These structures have been described as equal (Annandale, 1913) or subequal (Stubbings, 1936) in *S. longius* and unequal in *S. lambda* (Annandale, 1910). Caudal appendages of the Australian specimen are eight segmented. This structure appears to be similar in *S. lambda* (8 segments; Annandale, 1910) and *S. longius* (6 segments; Annandale, 1913; 8 segments; Stubbings, 1936).

The similarity of conchological and arthropodal characters support the conclusion that *S. longius* is a junior subjective synonym of *S. lambda*, as originally suggested by Annandale (1913) and later formalized - although not discussed - by Newman & Ross (1971) and Zevina (1981a). The Australian specimen collected by Cidaris I extends the geographical range of this species from the Indian Ocean to the waters of northeastern Queensland (Jones et al., 1990).

ARCOSCALPELLINAE Zevina, 1978
Verum Zevina, 1978

Verum australicum (Hoek, 1883)
(Figs 7,8)

Scalpellum australicum Hoek, 1883: 118, pl. 5, fig. 11; Weltner, 1922: 63.
Verum australicum: Zevina, 1981a: 223, Fig. 160.

Type Locality

Between New Guinea and Australia (12°08'S, 145°10'E); 'Challenger' station 184; 2561m; bottom temp. 1.8°C; substrate grey ooze.

Distribution

Zanzibar; between Australia and New Guinea. Depth range 463- 2561m. Now also recorded from northeastern Australia (1187- 1590m).

Material Examined

W*13239 (16°54'S, 137°14'E), 1473-1590m, 1 spec.; W*13240 (17°19'S, 147°11'E), 1402-1406m, 10 specs; W*13241 (17°20'S, 147°48'E), 1187-1200m, 1 spec.

Supplementary Description

Large individuals female. Capitulum oval, elongate, laterally compressed. Thirteen capitular plates, distinctly furrowed, closely approximate. Inframedian latus elongate, vase- shaped. Peduncle short, one-third to one-sixth capitular height, calcareous scales distinct, larger towards capitulum, arranged in five to six alternating rows. Measurements of the 12 specimens: CH 1.24-2.40 (mean 2.00), CW 0.58-1.35 (mean 1.06), PL 0.20-0.87 (mean 0.56), PW 0.09-0.68 (mean 0.52).

Cirrus I set apart from cirrus II, rami unequal,

FIG. 7. *Verum australicum* (Hoek, 1883). a, lateral view. b, cirrus I. c, intermediate segments, anterior ramus, cirrus II. d, distal segments, posterior ramus, cirrus III. e, intermediate segments, posterior ramus, cirrus V. f, proximal segments, posterior ramus, cirrus V. g, maxillule. h, mandible. i, j, lower angle of mandible. k, distal tip of caudal appendage.

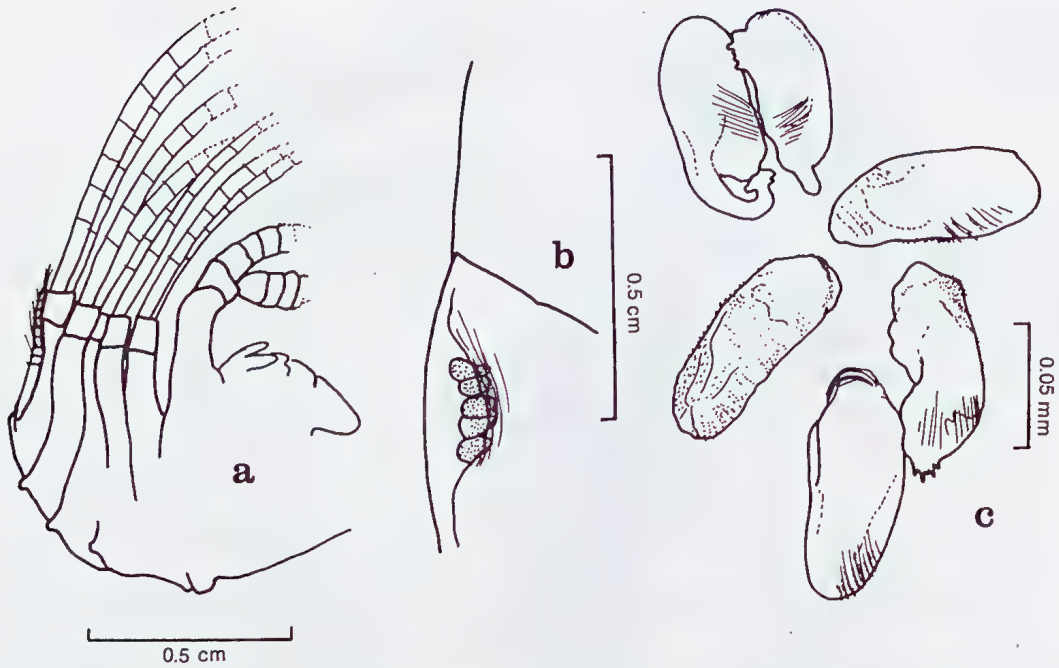

FIG. 8. *Verum australicum* (Hoek, 1883). a, lateral view of prosoma. b, dwarf males in scutal pocket. c, dwarf males.

anterior ramus shorter and much broader than posterior ramus, both rami densely setose. Cirri II to VI very long, cirri increasing in length to posterior, rami subequal, segments elongate, bearing four to five pairs of long setulate setae on anterior faces. Chaetotaxy ctenopod. Cirral formulae, see Table 5.

Maxillule with slight notch, four to five spines on cutting edge below notch, three stout subequal spines at upper angle, lower angle spinose. Mandible with three main teeth, lower angle pectinate, upper margin of third tooth with several small spines. Labrum extremely bullate, teeth absent. Caudal appendages short, marginally longer than pedicel of cirrus VI, multiarticulate (nine segments), long setae bearing fine setules distally. Penis absent. Dwarf males in pocket at occludent margin, on inner surface of and towards apex of right and left scuta of female, three to six males per pocket; males sac-like, ovoid, externally with chitinous spines, calcareous plates absent.

REMARKS

The material collected by Cidaris I extends the range of *V. australicum* into the waters of north-eastern Australia (Jones et al., 1990). The conchology of the specimens agrees in general with the original description of Hoek (1883). However, Hoek stated (p.118) that the 13 plates were 'closely locked together' and that there were 'no distinct interspaces between the different valves'. In the ontogenetic series of the Australian material an interspace develops between the carinal margin of the tergum and the upper portion of the carina in larger specimens (CH 2.20+). Hoek's type description was based on a smaller specimen (CH 1.25).

Hoek (1883) did not describe the internal structure of *V. australicum* and did not observe dwarf

TABLE 5. Measurements and cirral formulae of *Verum australicum* (Hoek, 1883).

CH	CW	PL	PW		CI	CII	CIII	CIV	CV	CVI	Ca
2.26	1.20	0.74	0.68	(R)	$\frac{8}{12}$	$\frac{17}{18}$	$\frac{20}{21}$	$\frac{26}{28}$	$\frac{25}{26}$	$\frac{26}{26}$	9
2.40	1.35	0.87	0.63	(R)	$\frac{9}{12}$	$\frac{18}{20}$	$\frac{23}{25}$	$\frac{27}{30}$	$\frac{29}{29}$	$\frac{31}{34}$	9

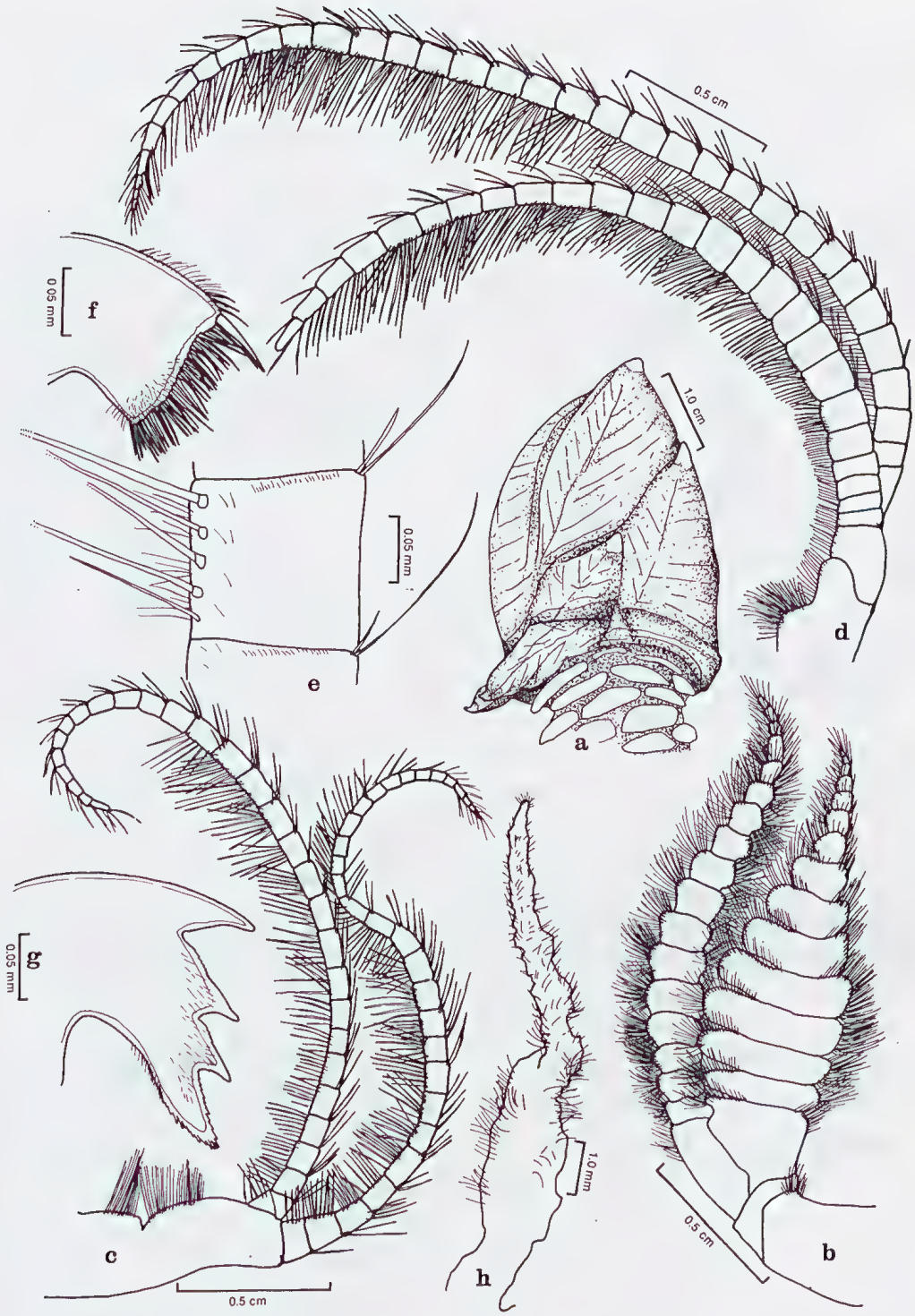

FIG. 9. *Anguloscalpellum pedunculatum* (Hoek, 1883). a, lateral view. b, cirrus I. c, cirrus II. d, cirrus III. e, intermediate segments, posterior ramus, cirrus IV. f, maxillule. g, mandible. h, penis.

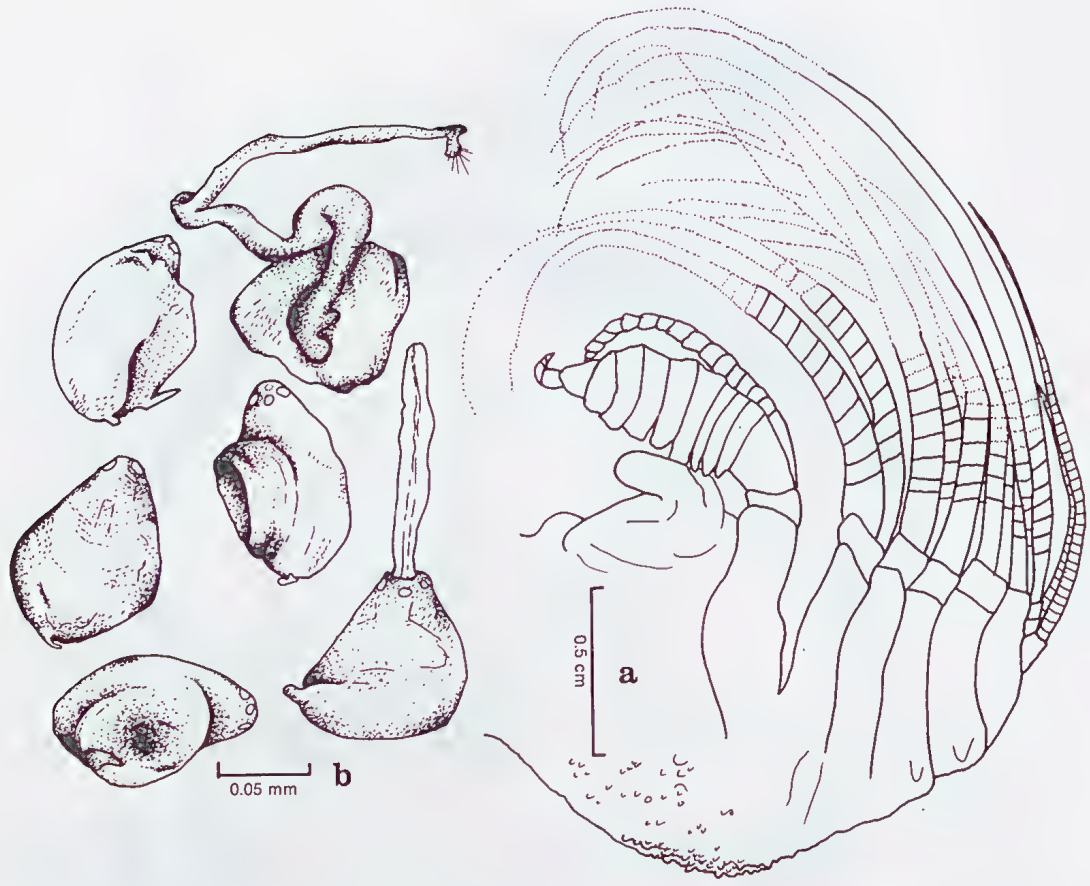

FIG. 10. *Anguloscalpellum pedunculatum* (Hoek, 1883). a, lateral view of prosoma. b, complemental males.

males. Details of cirri, mouthparts, caudal appendages and the penis, and observations of complemental males of the species are described here for the first time.

Anguloscalpellum Zevina, 1978

Anguloscalpellum pedunculatum (Hoek, 1883) (Figs 9,10)

Scalpellum pedunculatum Hoek, 1883: 99, pl. 6, figs 1-2.

Arcoscalpellum pedunculatum: Foster, 1978: 53, Pl. 7A, fig. 31.

Graviscalpellum peductulatum: Foster, 1980: 527, fig 3H.

Anguloscalpellum pedunculatum: Zevina, 1981a: 266, fig. 200.

TYPE LOCALITY

Pacific Ocean, near New Zealand (39°32'S, 171°48'E); 'Challenger' station 167; 274m; substrate grey ooze.

DISTRIBUTION

Western Pacific Ocean, New Zealand, Kermadecs, Norfolk I., central eastern Australia. Depth range 202-600m. Now also known from northeastern Australia (300-540m).

MATERIAL EXAMINED

W11222, E of Murray I. (09°51'S, 144°26'E), 480m, 2 specs; W*13242 (17°35'S, 146°53'E), 458-500m, 1 spec.; W10193, SE of Saumarez Reef (22°36'S, 154°14'E), 522m, 13 specs; W10192, 50 km NE Capricorn Gp (23°00'S, 153°00S, 153°18'E), 387m, 4 specs; W10191, 110 km E of Capricorn Gp (23°11'S, 153°00'E), 420m, 8 specs; W11324, E of Capricorn Gp (23°21'S, 153°23'E), 410m, 2 specs; W10190, 100 km

TABLE 6. Measurements and cirral formulae of *Anguloscalpellum pedunculatum* (Hoek, 1883).

CH	CW	PL	PW		CI	CII	CIII	CIV	CV	CVI	Ca
4.37	3.19	5.77	1.96	(R)	15/18	31/32	33/33	24/34	35/36	35/35	39
3.33	2.33	4.25	1.90	(R)	12/17	26/27	31/31	33/33	34/33	34/35	37

E of Capricorn Gp (23°30'S, 153°04'E), 540m, 29 specs; W11303 (part), E of Bunker Gp (23°54'S, 153°01'E), 465m, 2 specs; W11468, E of Bunker Gp (23°59'S, 152°59'E), 380m, 12 specs; W14334, off Morton I. (27°12'S, 153°52'E), 3 specs; W15351, off Morton I. (27°13'S, 153°52'E), 590m, 1 spec.; P35288 E of Gold Coast (28°02'-27°59'S, 153°59'E), 540m, 20 specs; P35290 E of Gold Coast (28°02'- 27°59'S, 153°59'E), 300m, 26 specs; P35289 E of Gold Coast (28°02'-05'S, 153°57'E), 360m, 1 spec.; P35208, E of Crowdy Head (32°06'-03'S, 153°04'-05'E), 360m, 1 spec.

SUPPLEMENTARY DESCRIPTION

Large individuals hermaphrodite. Capitulum subtriangular, inflated towards peduncle. Fourteen capitular plates, concealed by chitinous, hirsute membrane, apices projecting through membrane, plates of lower whorl short, small. Carinolatus elongated, subtriangular, extending outwards from capitulum laterally in larger specimens. Peduncle longer than capitulum, calcareous scales present, transversely elongated, arranged in alternating rows, covered by chitinous, hirsute membrane. Measurements of the 49 specimens: CH 2.68-4.68 (mean 4.05), CW 1.91-3.39 (mean 2.91), PL 4.60-12.97 (mean 8.19), PW 1.28-2.98 (mean 1.96).

Cirrus I slightly separated from cirrus II, rami unequal, proximal segments of anterior ramus wider than those of posterior ramus, strongly protuberant posteriorly, distal segments antenniform, segments of posterior ramus not protuberant. Cirri II to VI long, cirri increasing in length towards posterior, rami subequal, segments square, bearing four to seven pairs of long setae on anterior margins. Chaetotaxy ctenopod. Cirral formulae, see Table 6.

Maxillule with large spine at upper angle, cutting edge slightly sinuous, bearing numerous pairs of stout setae. Mandible with three large teeth, lower angle molariform, pectinated. Labrum extremely bullate, cutting edge straight with minute teeth. Caudal appendages multiarticulate, long (6-37 segments), half to two-thirds length of cirrus VI. Penis long, slender, tapering distally, sparsely setose, circlet of short dense setae at distal tip. Complemental males globulo-ovoid, orifice terminal, surrounded by four minute rudimentary plates, externally with chitinous spines in regular pattern, two prehensile antennae on ventral margin, extensile penis present; in shallow scutal pocket of hermaphrodite, three to four males per pocket, membrane of pocket with chitinous spines in regular pattern, membrane closely apposed to males.

REMARKS

Foster (1978, 1980) described material from New Zealand waters, Norfolk Island and the Kermadecs and mentioned that the species was also known to occur in the waters of eastern Australia (29°S), at a depth of 500-600m. Cidaris I speciemens of *A. pedunculatum* extended the known geographic range of the species northwards into the waters of north-eastern Queensland (17°S) (Jones et al., 1990) and material examined in the present study further extends the total range of the species from 32°S to Torres Strait (9°S).

Australian hermaphrodites agree well with published descriptions. The presence of a penis in the complemental male is confirmed and the orifice is terminal, rather than lateral as illustrated by Foster (1978) for New Zealand material. The close proximity of the scutal pocket membrane to the complemental males suggests the possibility of an interlocking function between the chitinous spines of the inner surface of the pocket and the external surface of the males, thus maintaining the males securely in the pouch.

Amigdoscalpellum Zevina, 1978
Amigdoscalpellum daschae Zevina, 1981
(Fig. 11)

Amigdoscalpellum daschae Zevina, 1981a: 290, fig. 219; 1981b: 87, fig. 9.

TYPE LOCALITY

SE of Papua New Guinea (11°30.5'S, 152°11.7'E); depth 3080m.

DISTRIBUTION

Type locality (3080m) and now also known from north- eastern Australia (1517-1564m).

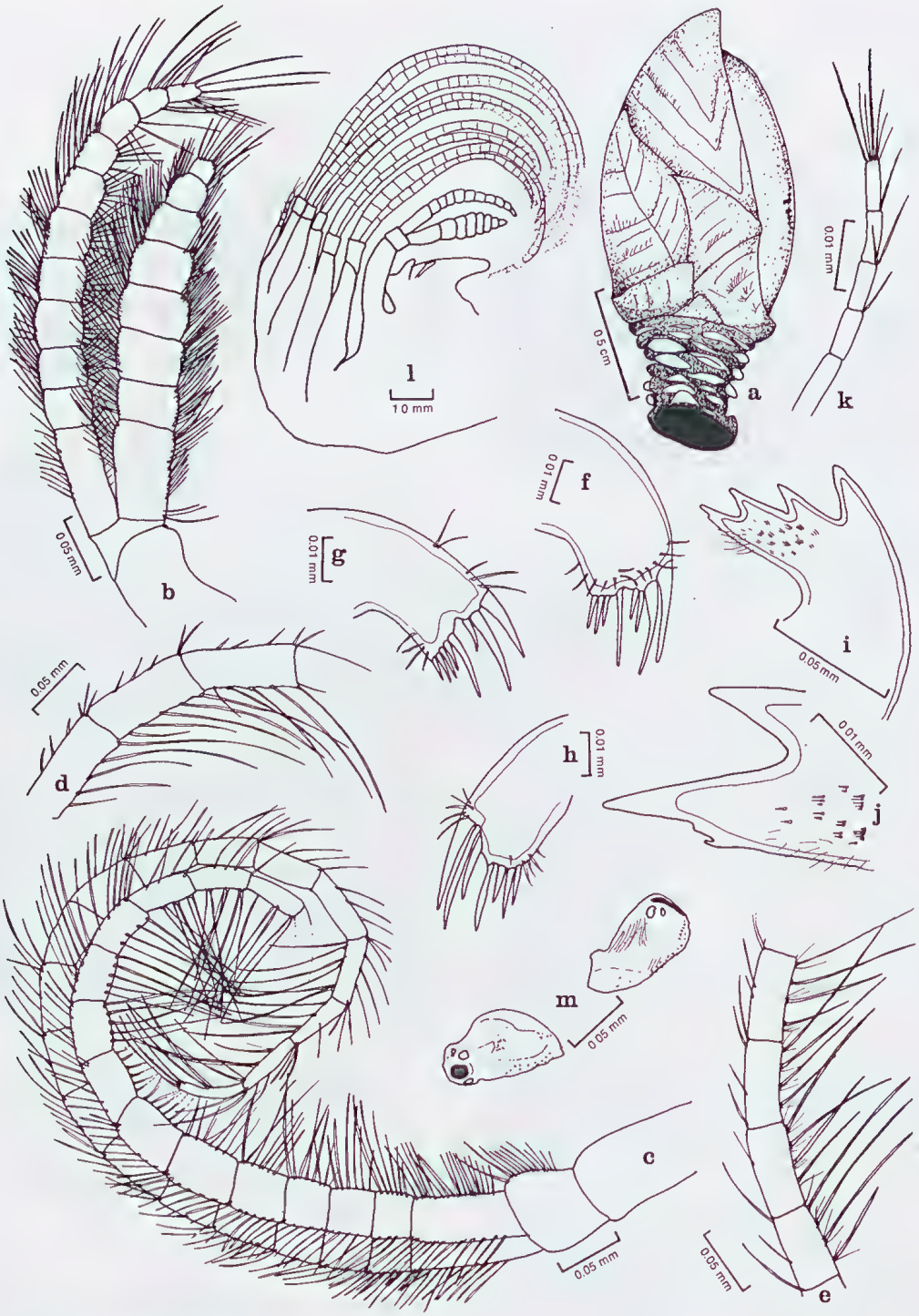

FIG. 11. *Amigdoscalpellum daschae* Zevina, 1981. a, lateral view. b, cirrus I. c, cirrus II. d, distal segments, posterior ramus, cirrus III. e, median segments, posterior ramus, cirrus V. f-h, maxillule. i, mandible. j, lower angle of mandible. k, distal tip of caudal appendage. l, lateral view of prosoma. m, dwarf males.

TABLE 7. Measurements and cirral formulae of *Amigdoscalpellum daschae* Zevina, 1981.

CH	CW	PL	PW		CI	CII	CIII	CIV	CV	CVI	Ca
1.21	0.76	0.53	0.43	(R)	7/8+	12+/13+	11+/12+	9+/10+	10+/10+	2+/10+	5
1.35	0.82	0.63	0.48	(R)	8/11	15+/20	20/22	22/25	23/26	25/24	5

TABLE 8. Measurements and cirral formulae of *Amigdoscalpellum elegans* (Hoek, 1907).

CH	CW	PL	PW		CI	CII	CIII	CIV	CV	CVI	Ca
2.05	0.90	0.46	0.43	(R)	9/12	19/21	26/26	27/28	28/28	29/32	1
1.37	0.65	0.25	0.35	(R)	8/10	17/19	23/23	regenerating			1

MATERIAL EXAMINED
W*13244 (16°59'S, 147°11'E), 1545-1564m, 1 spec; W*13243 (17°06'S, 147°12'E), 1517-1539m, 2 specs.

SUPPLEMENTARY DESCRIPTION
Large individuals female. Capitulum irregularly ovate, carinal margin more strongly curved than occludent margin. Thirteen capitular plates partially covered by thin, finely setose membrane, fine growth lines visible externally on all plates. Peduncle short, cylindrical, calcareous scales well developed, overlapping, arranged in alternate rows, covered with thin, finely setose membrane. Cirrus I much shorter than and set apart from cirri II to VI, anterior ramus shorter than and slightly wider than posterior ramus, both rami setose, especially inner surfaces. Cirri II to VI long, cirri increasing in length towards posterior, rami subequal, segments elongate, bearing four to five pairs long setae on anterior faces. Chaetotaxy ctenopod. Cirral formulae, see Table 7.

Maxillule with shallow median notch, two stout subequal setae at upper angle, one long seta and three pairs shorter setae below notch. Mandible with three main teeth, lower angle molariform with one or two small teeth on lower margin. Labrum bullate, cutting edge straight, teeth absent. Caudal appendages multiarticulate (5-6 segments), short, extending just beyond pedicel of cirrus VI, one twelfth length of cirrus VI, long setae bearing setules apically. Penis absent. Dwarf males in single row in shallow pocket at occludent margin, on inner surface of both scuta, towards apices; sac-like, four small rudimentary plates around terminal orifice, externally with small cuticular spines.

REMARKS
Material collected by Cidaris I extended the distribution of *A. daschae* into the waters of northeastern Australia (Jones et al., 1990). The form of the mandible of Australian specimens differs from that figured by Zevina (1981b). The pectination of the molariform lower angle, especially of the lower margin, is absent with only one or two small teeth or residual teeth present on the lower mandibular margin in Australian material.

Amigdoscalpellum elegans (Hoek, 1907) (Figs 12,13)

Scalpellum elegans Hoek, 1907: 107, pl. 8, fig. 9; Stubbings, 1936: 24.
Amigdoscalpellum elegans: Zevina 1981a: 268, fig. 201.

TYPE LOCALITY
Sulawesi (5°39'S, 122°12'E), 'Siboga' Station 208, 1886m, substrate solid green mud.

DISTRIBUTION
Indo-west Pacific - South Arabian coast, Sulawesi. Depth range 687-1886m. Now also known from northeastern Australia (687- 1228m).

MATERIAL EXAMINED
W*13245 (17°20'S, 147°48'E), 1187-1200m, 3 specs; W*13246 (18°04'S, 147°19'E), 687-704m, 1 spec.; W*13247 (17°45'S, 147°48'E), 1223-1228m, 2 specs; W*13248 (18°11'S, 148°22'E), 1109-1110m, 1 spec.

SUPPLEMENTARY DESCRIPTION
Large individuals female. Capitulum elongate, irregularly ovate, laterally compressed, carinal margin arched, occludent margin almost straight. Thirteen capitular plates, closely approximate, partially covered by thin, finely setose membrane, all plates except carina externally finely striated. Peduncle short, cylindrical, well-developed calcareous scales present, overlapping, arranged in rows, covered with thin, finely setose membrane. Measurements of the seven specimens: CH 0.89-

FIG. 12. *Amigdoscalpellum elegans* (Hoek, 1907). a, lateral view. b, cirrus I. c, distal segments, posterior ramus, cirrus I. d, distal segments, anterior ramus, cirrus II. e, intermediate segments, posterior ramus, cirrus II. f, cirrus II. g, intermediate segments, anterior ramus, cirrus V. h, intermediate segments, anterior ramus, cirrus VI. i, maxillule. j, mandible. k, lower angle of mandible.

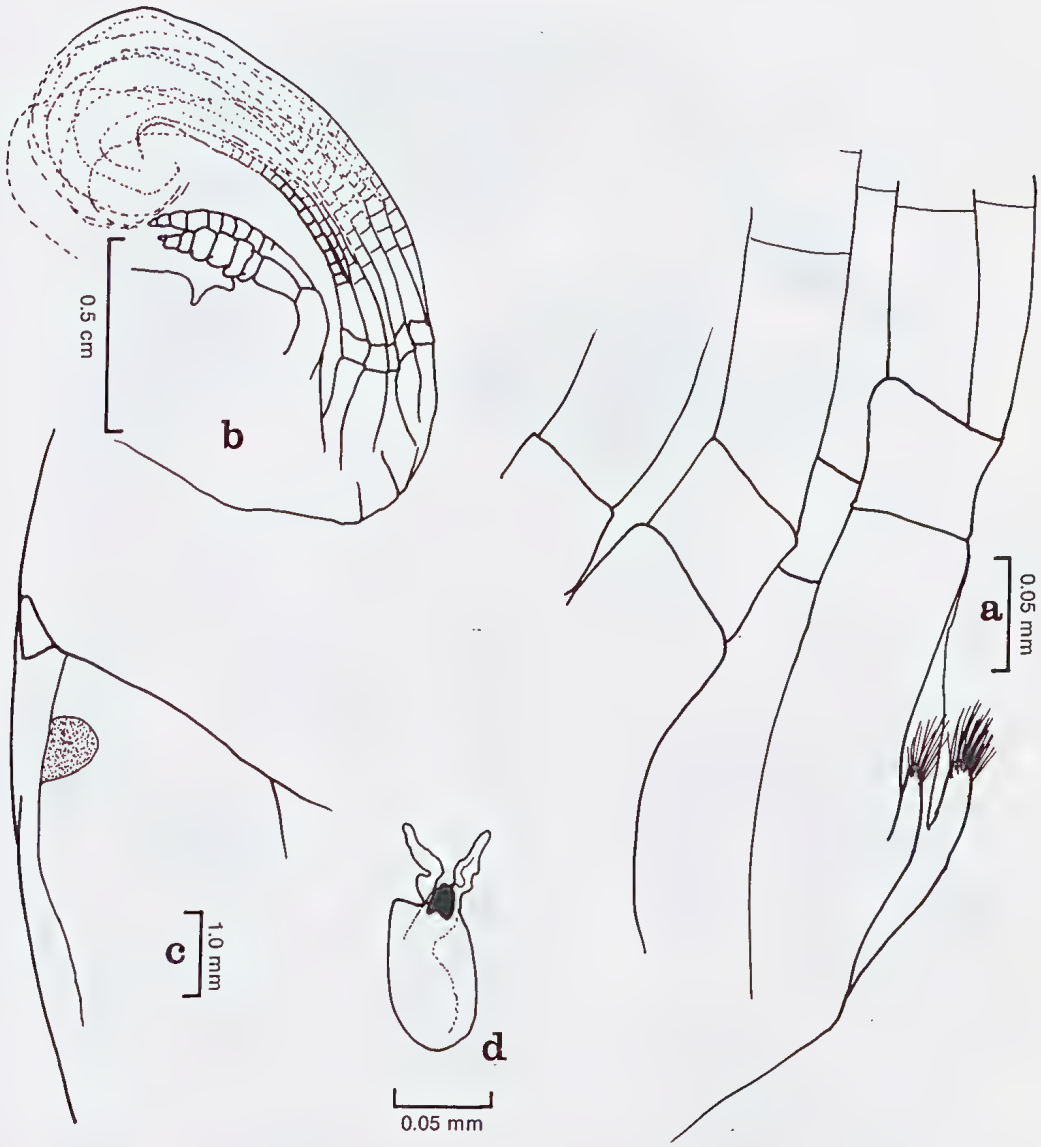

FIG. 13. *Amigdoscalpellum elegans* (Hoek, 1907). a, lateral view of prosoma to show caudal appendages. b, lateral view of prosoma. c, dwarf male in scutal pocket. d, dwarf male.

2.05 (mean 1.51); CW 0.39-2.05 (mean 0.69); PL 0.15-0.47 (mean 0.34); PW 0.14-0.48 (mean 0.35).

Cirrus I set above and slightly apart from remaining cirri, rami setose, anterior ramus shorter than posterior ramus, with intermediate segments broad but tending to antenniformy distally. Cirrus II with rami long, subequal, segments becoming elongate distally, anterior ramus more setose than posterior ramus. Cirri III to VI very long, rami subequal, segments elongate, bearing three to four pairs long setae on anterior margins. Chaetotaxy ctenopod. Cirral formulae, see Table 8.

Maxillule with small notch, definite, one stout spine at upper angle and one pair shorter setae above notch, three pairs of setae on cutting edge below notch, lowest pair longest, three pairs small setae towards lower angle. Mandible with three main teeth, lower angle coarsely pectinate, upper

FIG. 14. *Trianguloscalpellum hamulus* (Hoek, 1907). a, lateral view. b, rostrum. c, cirrus I. d, cirrus II. e, cirrus III. f, proximal segments, anterior ramus, cirrus V. g, distal segments, posterior ramus, cirrus VI.

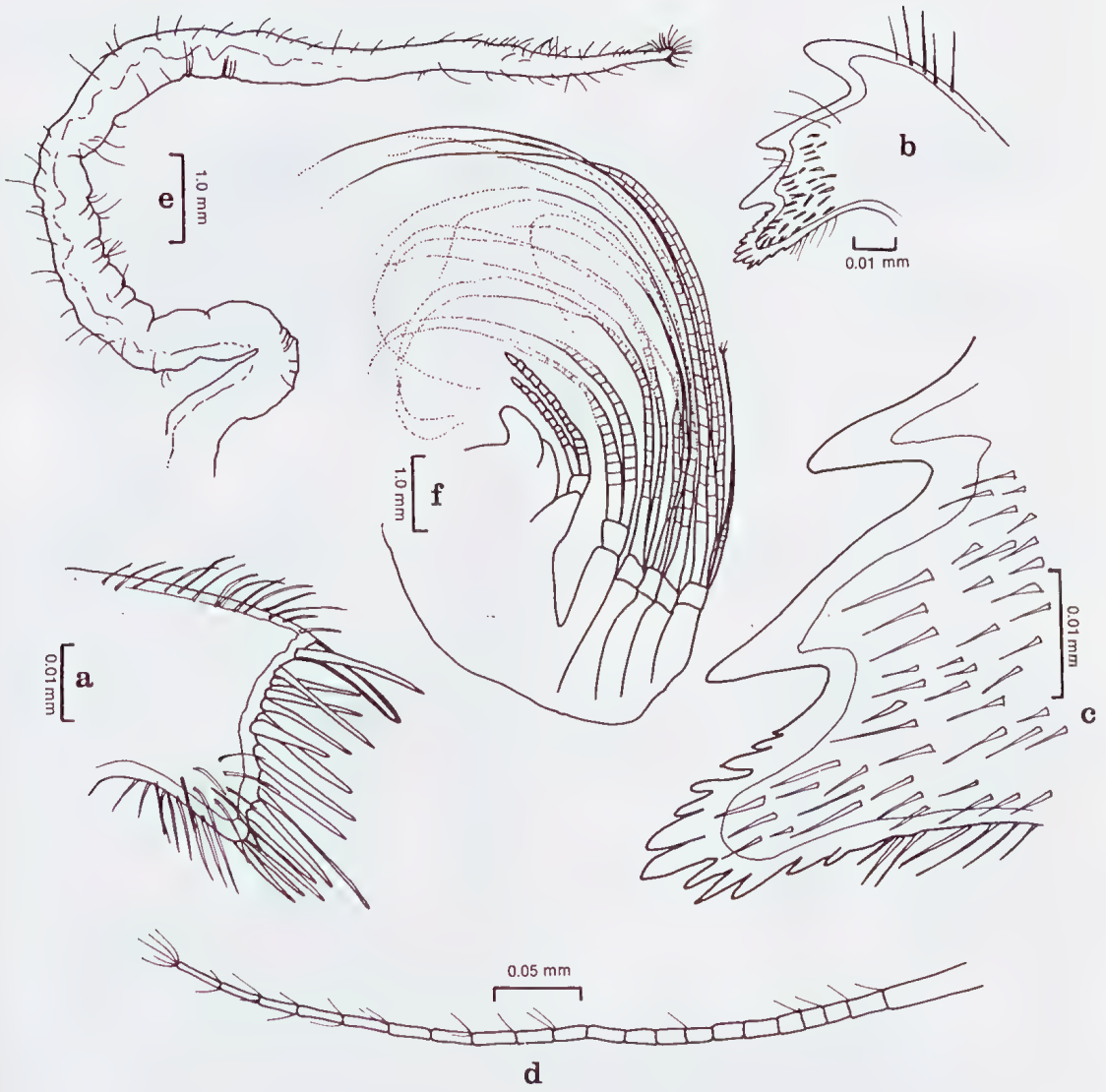

FIG. 15. *Trianguloscalpellum hamulus* (Hoek, 1907). a, maxillule. b, mandible. c, lower angle of mandible. d, caudal appendage. e, penis. f, lateral view of prosoma.

margin of third tooth with two small spines. Labrum bullate. Caudal appendages minute, less than one-quarter length of basal segment of pedicel of cirrus VI, with tuft of long setae apically. Penis absent. Dwarf male small, sac-like, four small rudimentary plates around terminal orifice; one specimen in shallow pocket at occludent margin towards apex of right scutum.

REMARKS

Material collected by Cidaris I extended the distribution of *A. elegans* into the waters of north-eastern Australia (Jones et al., 1990). This species appears to be rare, being known previously from only two specimens (Hoek, 1907; Stubbings, 1936). Conchological characters of the seven Australian specimens agree fairly closely with the original species description of Hoek (1907). The appendages of the female, and the dwarf males of *A. elegans* were undescribed prior to the present report.

TABLE 9. Cirral formula for *Trianguloscalpellum hamulus* (Hoek, 1907).

CH	CI	CII	CIII	CiV	CV	CVI	Ca
1.63	10/13	18/20	24/26	26/21+	25/25	27/27	21

Trianguloscalpellum Zevina, 1978
Trianguloscalpellum hamulus (Hoek, 1907)
(Figs 14,15)

Scalpellum hamulus Hoek, 1907: 86, pl. 7, fig. 14, 14a; Annandale, 1916b: 291.
Arcoscalpellum hamulus: Rosell, 1981: 281, pl. 1, figs a-d.
Trianguloscalpellum hamulus: Zevina, 1981a: 314, pl. 238.
Trianguloscalpellum hirsutum: Jones et al., 1990: 5 (*non T. hirsutum* (Hoek, 1883)).

TYPE LOCALITY
Banda Sea (5°26.6'S, 132°32.5'E); 'Siboga' station 256, 397m, bottom greyish green mud.

DISTRIBUTION
Banda Sea, Johul Bank (198 km S of Timor), Phillipines. Depth range 128-397m. Now also recorded from northeastern Australia (490-1119m).

MATERIAL EXAMINED
W*13249 (18°08'S, 148°15'E), 1115-1119m, 1 spec.; W*13250 (18°04'S, 147°17'E), 490-512m, 1 spec.; W10195, 130 km E of Capricorn Gp (23°28'S, 153°19'E), 562m, 1 spec.

SUPPLEMENTARY DESCRIPTION
Large individuals hermaphrodite. Capitulum elongate, ovate, apex slightly produced, occludent margin almost straight. Fourteen capitular plates, closely approximate, covered by thin, finely setose membrane. Peduncle short, cylindrical, well developed calcareous scales present, arranged in rows, covered with thin, finely setose membrane. Measurements as follows: CH 1.63, 0.83; CW 0.87, 0.35; PL 0.88, 0.25; PW 0.61, 0.30.

Cirrus I much shorter than cirri II to VI and set above and apart from remaining cirri, rami unequal, anterior ramus shorter and slightly wider than posterior ramus, rami setose, setae long, bearing setules. Cirri II to VI very long, cirri increasing in length towards posterior. Cirrus II with rami subequal, segments becoming elongate distally, anterior ramus more setose than posterior ramus, anterior faces of both rami bearing three to five pairs of long, setulate setae on anterior margins. Cirri III to VI with rami subequal, segments elongate, bearing three to four pairs of long setulate setae on anterior margins. Chaetotaxy ctenopod. Cirral formula, see Table 9.

Maxillule with slightly sinuous cutting edge bearing numerous small spines (10 to 12 pairs), upper angle with one stout spine, lower angle with short spines. Mandible with three main teeth, lower angle pectinate. Labrum extremely bullate. Caudal appendages very thin, long, one-quarter to one-third length of cirrus VI, multiarticulate (21 segments), circlet of fine setae apically. Penis long, thin, tapering distally, sparsely setose but setae more dense distally, circlet of fine setae apically.

REMARKS
This species appears to be comparatively rare. It was known previously from three specimens from the Philippines (Rosell, 1981), one from Indonesia (Hoek, 1907) and two from south of Timor (Annandale, 1916b). The three specimens collected by the Cidaris I expedition extended the known geographical range of *T. hamulus* to the waters of northern Queensland (Jones et al., 1990). The material agrees fairly closely with published conchological illustrations of the species (Hoek, 1907; Rosell, 1981). Only the larger of the two Cidaris I specimens was dissected. Details of arthropodal structures and mouthparts are described here for the first time as only the mandible has been figured previously (Rosell, 1981). Annandale (1916b) made brief mention of characters of the cirri and caudal appendages. The smaller (and presumably juvenile) specimen collected by the Cidaris I expedition is presently attributed to *T. hamulus*, based on conchology. However, the much deeper collection locality of this specimen has to be reckoned with. Until more specimens are collected and more information on the ontological development of this species is obtained, the identification cannot be confirmed. As has been the case with previous specimens, no complemental males were located in Australian material and these are yet to be described.

Arcoscalpellum Hoek, 1907

Arcoscalpellum michelottianum
(Seguenza, 1876) (Fig. 16,17)

Scalpellum michelottianum Seguenza, 1876: 381, 464, pl. 6, figs 15-25, pl. 10, fig. 26; de Alessandri, 1895:

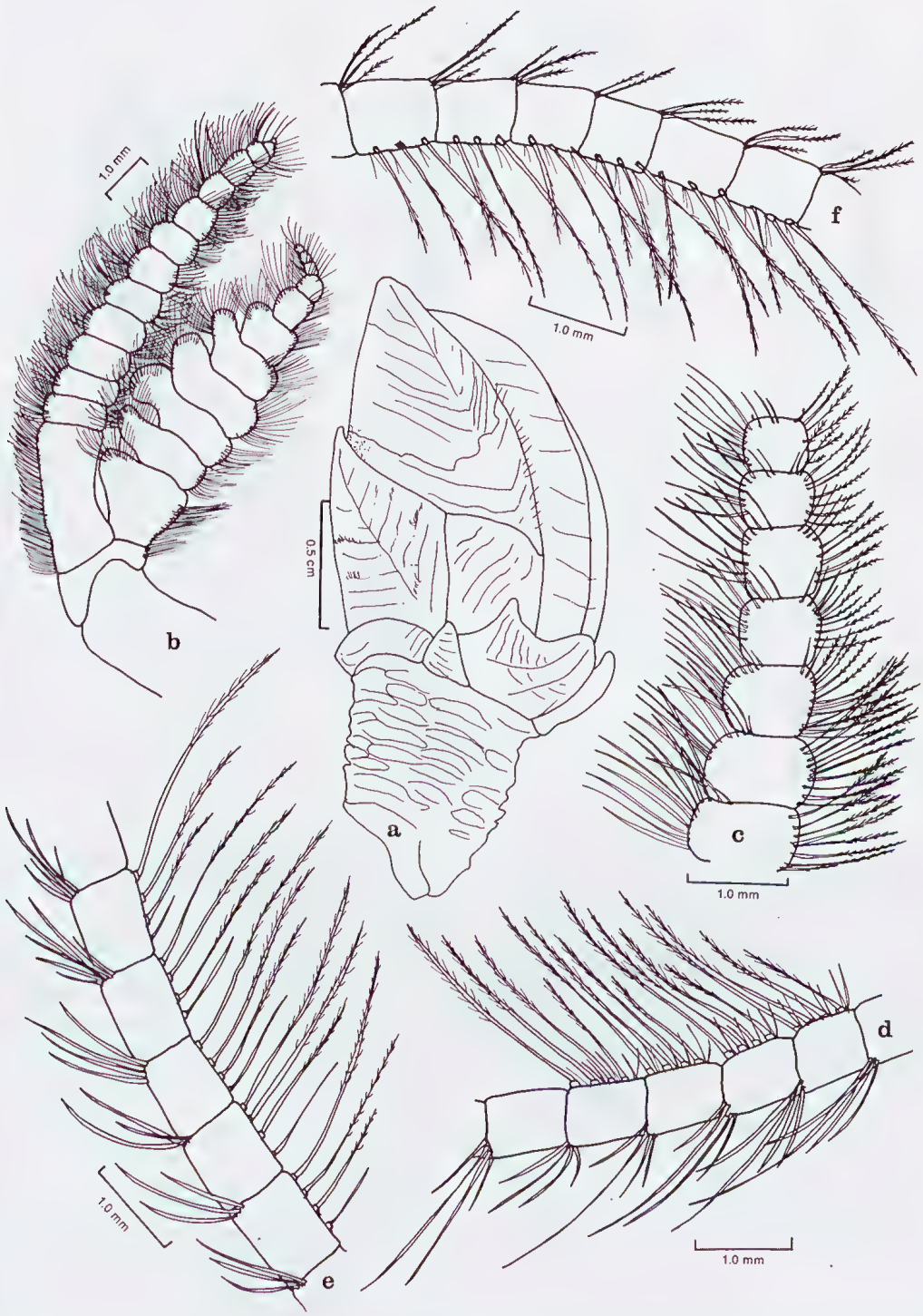

FIG. 16. *Arcoscalpellum michelottianum* (Seguenza, 1876). a, lateral view. b, cirrus I. c, intermediate segments, anterior ramus, cirrus II. d, intermediate segments, posterior ramus, cirrus II. e, intermediate segments, anterior ramus, cirrus III. f, intermediate segments, anterior ramus, cirrus V.

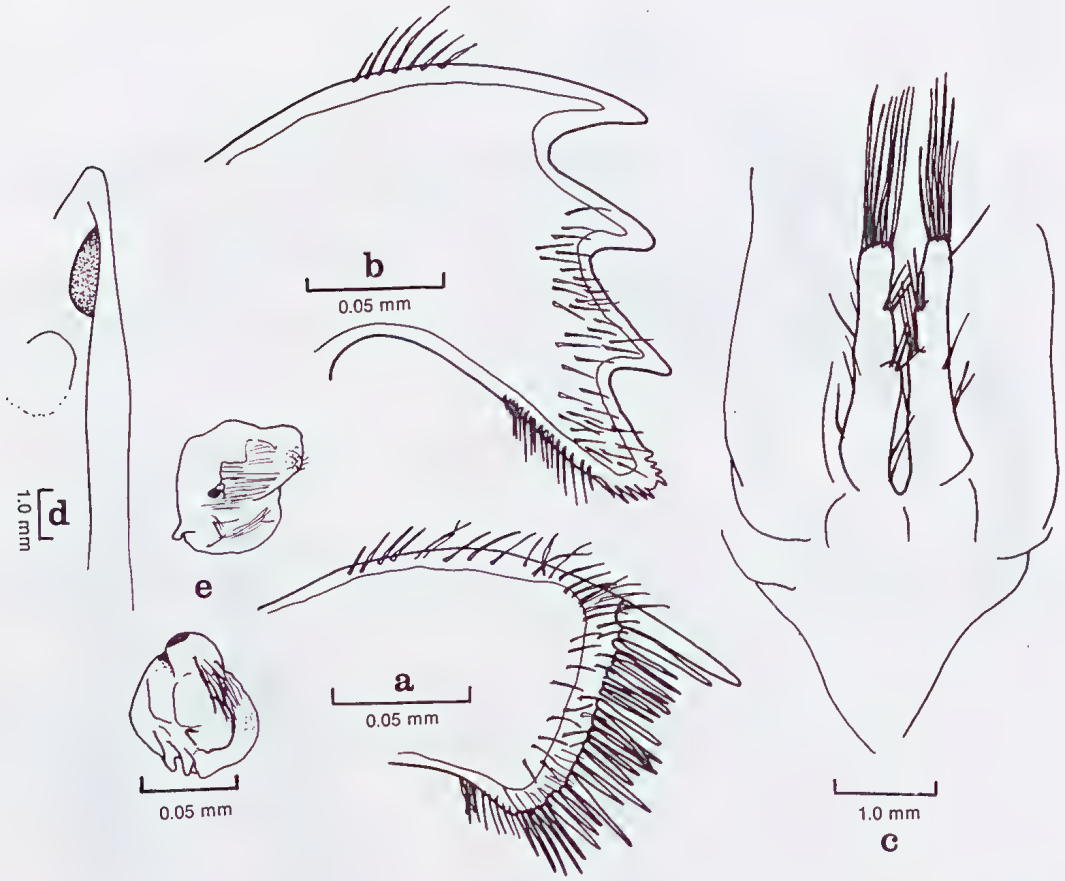

FIG. 17. *Arcoscalpellum michelottianum* (Seguenza, 1876). a, maxillule. b, mandible. c, posterior view, caudal appendages and pedicels of posterior cirri. d, dwarf male in scutal pocket. e, dwarf males.

263 (in part); 1897: 47; 1906: 251; Withers, 1953: 225.

Scalpellum velutinum Hoek, 1883: 96, pl. 4, figs 10-11, pl. 9, figs 7-9; Gruvel, 1902: 56, 136, pl. 2, figs 3c, 10a-b, 14, pl. 3, figs 1, 27-31, pl. 4, figs 6, 11-22; 1905: 73, fig. 83; Annandale, 1906a: 389; Pilsbry, 1907: 26, pl. 3, figs 2-3; Annandale, 1908: pl. 4, fig. 7; 1911: 588; Gruvel, 1912: 2; Annandale, 1913: 229; Hoek, 1914: 4; Calman, 1918: 108; Gruvel, 1920: 27, pl. 1, figs 8-10, pl. 7, fig. 4; Weltner, 1922: 75; Nilsson-Cantell, 1927: 743, fig. 1; 1928: 4; Broch, 1931: 18; Nilsson-Cantell, 1931: 7; Stubbings, 1936: 28, fig. 12; Tarasov & Zevina, 1957: 24, fig. 9H; Stubbings, 1967: 234; Zevina, 1972: 43, fig. 2.

Scalpellum eximium Hoek, 1883: 100, pl. 4, figs 6-7, pl. 9, fig. 10; Weltner, 1897: 247.

Scalpellum sordidum Aurivillius, 1898: 190.

Scalpellum erectum Aurivillius, 1898: 192; Gruvel, 1905: 74.

Scalpellum alatum Gruvel, 1900: 192, 1902: 57.

Arcoscalpellum michelottianum: Newman & Ross, 1971: 71, fig. 34, pl. 9B; Lakshmana Rao & Newman, 1972:76, fig. 5; Zevina 1981a: 343, fig. 263.

Trianguloscalpellum michelottianum: Liu & Ren, 1985: 207, fig. 14, pl. 4, figs 10-12; Ren, 1989: 442, fig. 6.

TYPE LOCALITY

Unknown.

DISTRIBUTION

Atlantic Ocean; Indian Ocean; Malay Arch.; Pacific Ocean; Chile. Depth range 64-5190m. Now also known from northeastern and northwestern Australia (458-736m).

MATERIAL EXAMINED

W*13251 (17°52'S, 147°08'E), 497-503m, 1 spec.; W*13252 (17°35'S, 146°53'E), 458-500m, 1 spec.;

TABLE 10. Measurements and cirral formulae of *Arcoscalpellum michelottianum* (Seguenza, 1876).

CH		CI	CII	CIII	CIV	CV	CVI	Ca
1.68	(L)	7/10	19/20	22/23	24/17+	24/25	25/25	1(2)*
	(R)	8/10	18/20	22/23	24/24	23/25	23/25	1(2)*
1.68	(L)	11/14	15+/17+	25/22				1(3)*
	(R)	11/7+	14+/19+	31/7+	5+/20	24+/24+		1(3)*

* segements not distinct

WAM 935-86 NW of Port Hedland (18°37'S, 116°40'E), 732- 736m, 1 spec.

SUPPLEMENTARY DESCRIPTION

Large individuals female. Capitulum subtriangular, 14 capitular plates, approximate, fully calcified, covered by thin, pale brown, chitinous membrane, sparsely hairy, apices of plates projecting freely through membrane, growth lines faint. Peduncle one-quarter to one-third capitular height, well-developed calcareous scales present, arranged in alternating rows. Measurements of the three specimens: CH 0.96, 1.68, 3.05; CW 0.56, 1.05, 2.43; PL 0.44, 0.88, broken; PW 0.31, 0.61, broken.

Cirrus I with rami unequal, posterior ramus longer than anterior ramus, anterior ramus with intermediate segments protuberant posteriorly, both rami with many long, finely setulate setae, especially on inner surfaces. Cirrus II longer than cirrus I, rami subequal, anterior ramus more densely setose than posterior ramus, long setae finely setulate. Cirri III to VI elongate, cirri increasing in length towards posterior, rami subequal, segments elongate bearing three to four pairs of long, setulate setae on anterior margins. Chaetotaxy ctenopod. Cirral formulae, see Table 10.

Maxillule without definite notch but slight indentation apparent below upper angle, one stout spine at upper angle, cutting edge below indentation almost straight with many paired setae. Mandible with three teeth, molariform lower angle pectinate. Labrum extremely bullate. Caudal appendages stout, approximately one- half to two-thirds length of basal segment of pedicel of cirrus VI, two- or three-segmented but segments indistinct, setulate setae terminally. Penis absent. Dwarf males globulo-ovoid, orifice terminal, calcareous plates absent, a pair of antennae at opposite pole to orifice, outer surface with muscle striations, not covered with spicules arranged in transverse rows but by minute spiniferous excrescences; in pocket at occludent margin, on inner surfaces of right and left scuta of female just above adductor muscle pit of scuta, one male per pocket.

REMARKS

The considerable range of variation exhibited by this wide-ranging species has been noted by various authors (e.g. Gruvel, 1902; Calman, 1918; Newman & Ross, 1971). The two specimens collected by Cidaris I were the first records of *A. michelottianum* from the waters of eastern Australia (Jones et al., 1990).

However the identification is provisional. Of the three specimens examined, only the middle-sized specimen (CH 1.68) was dissected. Differences and similarities of this material to published descriptions of *A. michelottianum* are discussed below.

Australian material shows the maxillule without a notch, but with a slight indentation below the upper angle. Newman & Ross (1971), examining slightly smaller specimens, interpreted a similar but slightly more pronounced indentation as evidence for a distinct notch in the maxillule. However, for a larger specimen (CH 3.0) Nilsson-Cantell (1927) described the cutting edge of the maxillule as nearly straight, although Newman & Ross (1971) suggested an indication of a slight notch in Nilsson-Cantell's illustration of this appendage. Zevina (1972) showed no distinct notch but illustrated a more sinuous configuration to the cutting edge than described previously. Lakshmana Rao & Newman (1972) found no supramedian notch on the cutting edge of the maxillule in mid- Pacific material.

Segmentation of the caudal appendages of young specimens of *A. michelottianum* is indistinct but larger specimens show distinct segmentation (e.g. Gruvel, 1902: 7-8 segments; Calman, 1918: 4-6 segments; Nilsson-Cantell, 1927: 7 segments; Zevina, 1972: 1-6 segments; Lakshmana Rao & Newman, 1972: 2-4 segments). Australian material exhibits indistinctly two- segmented (CH 1.68) or three-segmented (CA 3.05) caudal appendages. This character appears to vary with age.

The posterior cirri of the medium-sized Australian specimen bear four pairs of long, setulate setae along the anterior margins of the intermediate segments. Newman & Ross (1971) figured three pairs per segment for slightly smaller animals and Nilsson-Cantell (1927) and Lakshmana Rao & Newman (1972) described four pairs per segment for larger specimens; this difference may, therefore, be attributable to age.

All three Australian specimens show carinolatera projecting beyond the carinal edge of the capitulum, the projection being strongest in the larger specimen. This condition is not illustrated by Newman & Ross (1971), whose material (CH 1.18-0.32) covers the size range of the smallest Australian specimen. The original illustration of *S. velutinum* (Hoek, 1883) showed the carinolatera projecting beyond the capitulum and this condition is also illustrated by Gruvel (1902, 1905) and Zevina (1972). These plates, however, may only slightly project from the capitulum (Hoek, 1883 as *S. eximium*; Nilsson- Cantell, 1927). The degree of projection appears to be variable, reflecting different stages in ontogenetic development.

Conchology of the two larger Australian specimens is very similar to that figured for Chilean specimens (CH 3.1-1.6) of *S. velutinum* (Zevina, 1972), although the peduncular scales appear more developed (i.e. larger in size and closely approximate) in the Australian examples. It must be noted that the conchology of the smallest Australian specimen, presently assigned to *A. michelottianum*, is also very similar to that illustrated by Ultinomi (1968) for *S. hirsutum* (CH 1.3, CW 0.9). This author commented that externally the female capitulum of *S. hirsutum* closely resembled *S. velutinum* but that characters of the maxillule (a distinct small notch below the upper angle), mandible (pectination of the upper margin of the third mandibular tooth) and the dwarf male (minute spiniferous excrescences on surface) warranted specific separation. However, the dwarf males of the Australian material herein ascribed to *A. michelottianum* exhibit similar surface spiniferous excrescences rather than cuticular hairs. *S. hirsutum* is only known from two specimens - the Arafura Sea, 390m (Utinomi, 1968) and the Moluccan Sea, 1485m (Hoek, 1883). Ren (1983) described *A. ciliatum* from the East China Sea. It shows conchological characters very similar to *A. michelottianum*. He also synonymized *S. hirsutum* (Utinomi, 1968) but not *S. hirsutum* sensu Hoek, 1883 with *A.* ciliatum. Differences in the caudal appendages (uniarticulate, expanded oval-shaped) and the maxillule (notched) distinguish *A. cilitum* from *A. michelottianum*. Dwarf males of *A. ciliatum* remain to be described.

Arcoscalpellum moluccanum (Hoek, 1883)
(Figs 18,19)

Scalpellum moluccanum Hoek, 1883: 104, pl. 5, Figs 3-4; 1907: 56, 85, pl. 7, fig. 13; Gruvel, 1905: 76, fig. 85; Nilsson-Cantell, 1927: 747 fig. 3.
Arcoscalpellum moluccanum: Newman & Ross, 1971: 60.

TYPE LOCALITY

Banda Sea (4°21'S, 129°7'E), 'Challenger' station 195, 2606m, bottom temp. 3.0°C, substrate grey ooze.

DISTRIBUTION

Indonesia, Tasman Sea. Depth range 788-2745m. Now also known from northeastern Australia (904-1491m).

MATERIAL EXAMINED

W*13253 (17°20'S, 147°48'E), 1187-1200m, 7 specs; W*13254 (17°51'S, 147°09'E), 904-916m, 1 spec.; W*13255 (17°12'S, 147°11'E), 1489-1491m, 1 spec.

SUPPLEMENTARY DESCRIPTION

Large individuals female. Capitulum subtriangular, inflated. Fourteen capitular plates, covered by relatively thin chitinous membrane, sparsely hirsute, apices of plates projecting freely through membrane, growth lines fairly distinct. Peduncle stout, narrowing towards base, shorter than capitulum, well- developed calcareous scales present, arranged in alternating rows. Measurements of the seven specimens: CH 1.78-2.09 (mean 1.91); CW 1.10-1.33 (mean 1.22); PL 0.99 - 1.46 (mean 1.23); PW 0.87 - 1.17 (mean 1.02).

Cirrus I set apart from cirrus II, stouter and much shorter than cirri II to VI, anterior ramus shorter than posterior ramus, intermediate segments of anterior ramus strongly protuberant posteriorly, segments of posterior ramus not protuberant, both rami setose, especially posterior faces and medial faces of anterior ramus. Cirri II-VI elongate, rami subequal, cirri increasing in length towards posterior. Cirrus II with three to four pairs of setae along anterior border of segments, anterior ramus more setose than posterior ramus, posterior surfaces of both rami setose. Cirri III and IV with anterior and posterior rami with two to four pairs of setae along anterior margins of segments, posterior surfaces of segments sparsely setose.

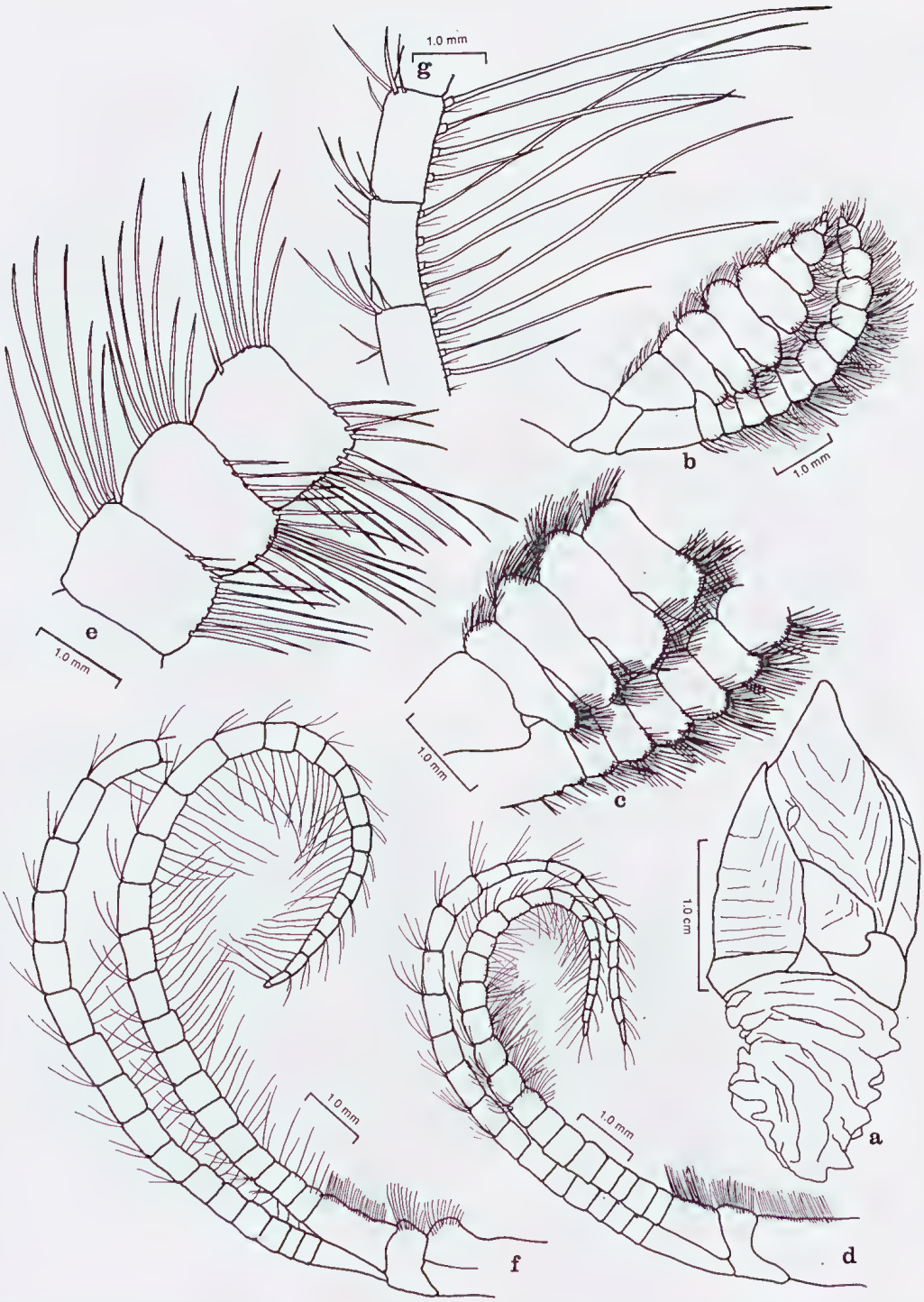

FIG. 18. *Arcoscalpellum moluccanum* (Hoek, 1883). a, lateral view. b, cirrus I. c, proximal segments, cirrus I. d, cirrus II. e, intermediate segments, anterior ramus, cirrus II. f, cirrus III. g, intermediate segments, posterior ramus, cirrus III.

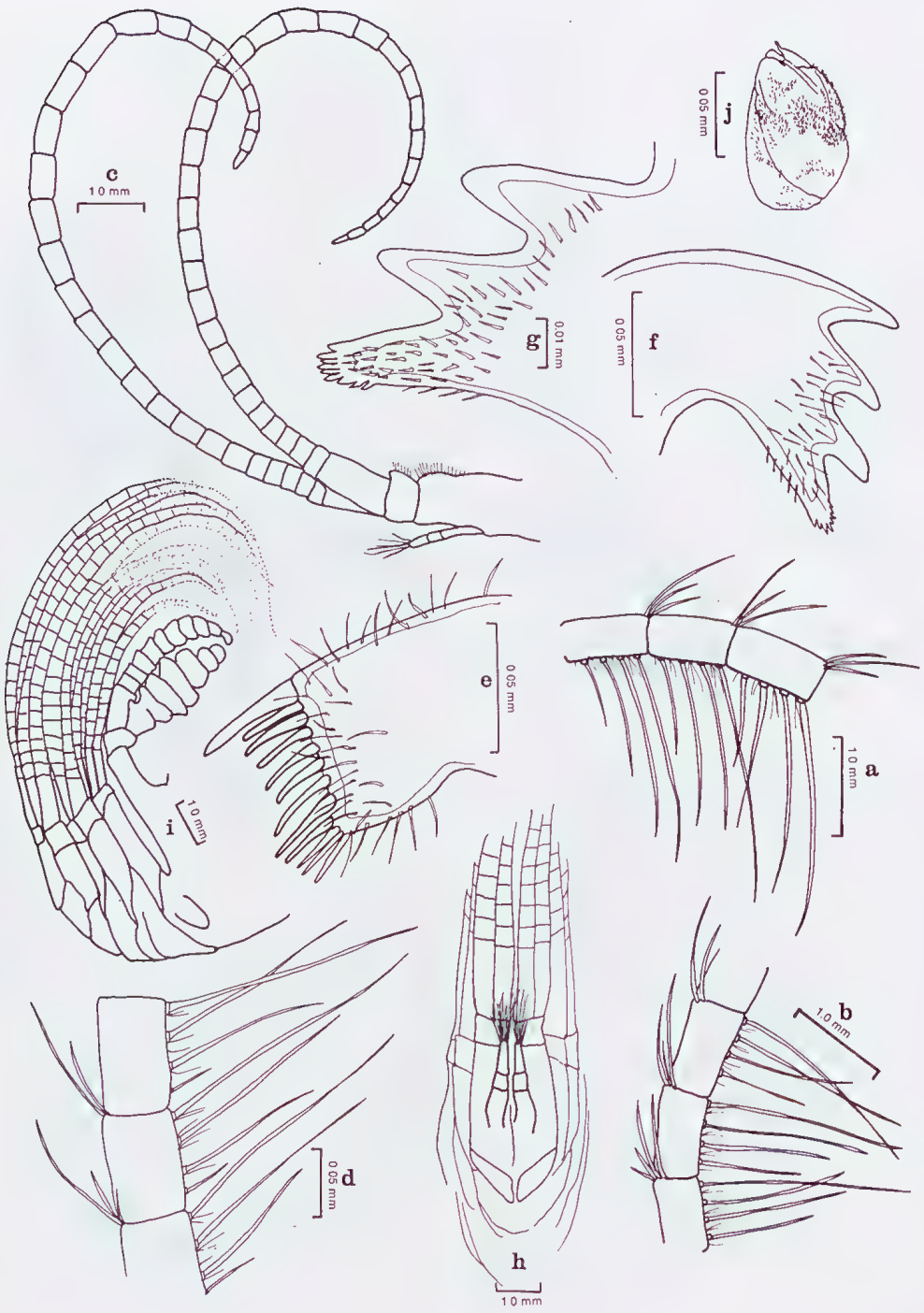

FIG. 19. *Arcoscalpellum moluccanum* (Hoek, 1883). a, intermediate segments, anterior ramus, cirrus IV. b, intermediate segments, posterior ramus, cirrus V. c, cirrus VI. d, intermediate segments, posterior ramus, cirrus VI. e, maxillule. f, mandible. g, lower angle of mandible. h, posterior view, caudal appendages and pedicels of posterior cirri. i, lateral view of prosoma. j, dwarf male.

TABLE 11. Measurements and cirral formulae of *Arcoscalpellum moluccanum* Hoek (1883).

CH	CW	PL	PW		CI	CII	CIII	CIV	CV	CVI	Ca
2.05	1.33	1.33	1.10	(R)	9/13	24/25	29/30	29/30	31/28	33/29	3
				(L)	10/13	24/26	29/25+	26+/30	31/30	31/32	3

Cirri V and VI with four pairs of setae along anterior margins of segments, posterior surfaces of both rami sparsely setose. Chaetotaxy ctenopod. Cirral formulae, see Table 11.

Maxillule without notch, large stout spine at upper angle, cutting edge almost straight, bearing seven to eight pairs of setae, lower angle slightly protuberant, bearing five pairs of setae. Mandible with three large teeth, lower angle pectinated. Labrum extremely bullate, cutting edge straight, teeth absent. Caudal appendages slightly longer than basal segment of pedicel of cirrus VI, three-segmented, several long, stiff setae distally. Penis absent. Dwarf males small, elongate, ovoid, externally covered with chitinous, short, stout setae, antennae present, rudimentary plates around orifice lacking; in pouch inside occludent margin of right scutum of female, at base of occludent orifice, just above adductor muscle.

REMARKS

The species was previously known from four specimens (Hoek, 1883, 1907; Nilsson-Cantell, 1927) and only their conchology has been described. The nine Australian specimens collected by Cidaris I constitute the first records of *A. moluccanum* in Australian waters (Jones et al., 1990). They agree closely with the original description of *A. moluccanum* (Hoek, 1883). The conchology of both the Atlantic species *T. regium* (Thomson) and the Antarctic and eastern Pacific *A. darwinii* (Hoek) is very similar to that of *A. moluccanum*.

The form of the carinolatera, especially where they meet at the base of the carina, and the position of the rostrum relative to the rostrolatera, separate *A. moluccanum*, *A. darwinii* and *T. regium*. The internal anatomy of *A. moluccanum* described above is similar to previous brief descriptions of these parts for *T. regium* (Hoek, 1883; Pilsbry, 1907). Descriptions of the dwarf males of *T. regium* (Hoek, 1884) are more similar to those *A. moluccanum* than to *A. darwinii*. The mouthparts and the caudal appendages (three segmented in *A. moluccanum*, 4 to 6 segmented in *T. regium*, four to five segmented in *A. darwinii*) are similar in all three species. It is possible that *A. moluccanum* may be a geographical 'race' as suggested by Hoek (1883). Until comparison of the type material of *A. regium* and *A. moluccanum* can be made, the identity of the Australian specimens is tentative.

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DISTRIBUTION OF THE LONG-NECKED FRESHWATER TURTLE *CHELODINA NOVAEGUINEAE* AND NEW INFORMATION ON ITS ECOLOGY

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Kennett, R.M., Georges, A., Thomas, K. & Georges, T.C. 1992 06 29. Distribution of the long-necked freshwater turtle *Chelodina novaeguineae* and new information on its ecology. *Memoirs of the Queensland Museum* **32**(1): 179-182. Brisbane. ISSN 0079-8835.

Recent collections have extended the westerly distribution of *Chelodina novaeguineae*. The species occupies semi-permanent and seasonally ephemeral waterholes from coastal northeast Queensland to the Daly Waters region of the Northern Territory. *C. novaeguineae*, along with *C. longicollis* and *C. steindachneri*, may have speciated from a common ancestor whose widespread distribution around the periphery of the continent covered the present distribution of these species. *C. novaeguineae* aestivates or migrates overland to permanent water when the waterhole it occupies dries. Its reproductive pattern of dry season nesting, small egg size and long incubation period conflicts with a current interpretation of the phylogeny of Australian chelid turtles. □*Chelidae, Chelodina novaeguineae, ecology, distribution.*

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7 November, 1991.

Chelodina novaeguineae was first described from the Binaturi River in New Guinea (Boulenger, 1888) and later found to occur also in north-eastern Queensland, Australia (Goode, 1967). Its distribution in Australia is poorly known. Covacevich and Couper (1991) provide a map showing its Queensland distribution based on specimens held in the Queensland Museum and these data together with anecdotal reports (Goode, 1967; Cann, 1978) suggest it is distributed not only on Cape York Penninsula but throughout the Gulf of Carpentaria, in Arnhem Land, and as far south as Newcastle Waters in the Northern Territory. More recent collections (King & Horner, 1987; Covacevich et al., 1990) confirm that the species' distribution extends into the Gulf country of western Queensland and the Northern Territory.

In this note, we provide a range extension for *C. novaeguineae*, review museum specimens to provide an updated map of the distribution of the species, and provide new information on its ecology.

RESULTS

On 29 April, 1990, we collected two live specimens and three shells of *C. novaeguineae* from Malogie Waterhole, a small permanent waterhole in the Roper River catchment near Scarlet Hill on Kalala Station (16°8'S 133°36'E) in the Northern Territory. Another three shells were collected from Stuart Swamp near the township of Daly Waters (16°14'S 133°27'E) (Table 1). The specimens were determined to be *C. novaeguineae* on the basis of the following characters:

- The plastron is greatly expanded anteriorly, less than 1.9 times longer than broad (unlike *Chelodina rugosa*, *C. expansa* and *C. oblonga*), but extends barely as far as the inner edges of the overlying marginal plates of the carapace (unlike *C. longicollis*).
- The intergular shield is markedly more than twice as long as the suture between the pectoral shields (unlike *C. rugosa*, *C. expansa* and *C. oblonga*).
- The common boundary of the 12th marginals is not raised to form a distinct inverted 'V' when viewed from the rear (unlike *C. longicollis*).
- The carapace is broadly oval (unlike *C. steindachneri*).

Stuart Swamp drains into Daly Waters Creek in the upper catchment of the Roper River. When full, the swamp covers several square kilometres but poor wet season rainfall over the previous three years had reduced the waterhole to a relatively small muddy hole about 75m in diameter at the time of our visit. The waterhole dried completely a few months later for the first time in many

TABLE 1. Details of *Chelodina novaeguineae* collected from Kalala Station, Northern Territory, April 1990.

Location where specimen is held	Specimen number	Carapace length	Carapace width	Plastron length	Plastron width	Shell depth	Sex
NT Museum	NTMR 16324	210	169	169	110	79	—
	NTMR 16325	230	188	190	118	88	—
Qld Museum	J 53635	231	175	181	118	74	—
R. Kennett (pers. coll.)		209	170	175	—	74	—
Australia Museum	R 132784	199	161	159	101	74	—
	R 132785	235	184	190	116	77	—
	R 135351	193	156	157	98	65	F

years (Bill Cook, Kalala Station, pers. comm.). Malogie Waterhole was the only waterhole in the area to retain water in 1990, while many others dried for the first time in living memory (Bill Cook, pers. comm.).

The turtles were transported to Canberra where abdominal palpation on 26 May, 1990 revealed the female to be gravid. Nine hard-shelled (calcareous) eggs were obtained on 28 May, 1990 by inducing oviposition with an injection of synthetic oxytocin (Ewert & Legler, 1978). A tenth egg was found in the holding tank weeks later but was not measured. Mean egg length was 31.4±0.2mm, egg width was 21.8±0.1mm and egg weight was 8.6±0.1g (mean, standard error, n=9). The eggs were incubated at 30°C in a plastic container on a bed of vermiculite moistened to a constant ratio of 4g vermiculite to 3g water. An opaque white patch appeared on each of the nine eggs within 36 hours indicating development had commenced (Thompson, 1985) and the eggs hatched on 25 September, 1990, 120 days later. Mean hatchling carapace length was 31.3±1.0mm, mean carapace width was 26.6±0.4mm and mean weight was 5.4±0.3g (mean, standard error, n=3).

DISCUSSION

Recent collections of *C. novaeguineae* (King & Horner, 1987; Covacevich et al., 1990; this paper) have substantially increased the known Australian range of the species. Formerly only known from northeast Queensland (Cogger, 1988), *C. novaeguineae* has now been recorded from the Gulf country near the Queensland and Northern Territory border (Covacevich et al., 1990) and from Maria Island in the Gulf of Carpentaria (King & Horner, 1987). King & Horner (1987) suggest that the population on Maria Island in the Gulf of Carpentaria may have been established by turtles swept out of rivers during flooding in either the Roper, Towns or Limmen-Bight Rivers. Our finding of *C. novaeguineae* in the upper reaches of the Roper River, is consistent with this suggestion and confirms Cann's (1978) reports of *C. novaeguineae* in the Daly Waters area and his reference to their presence in the lower reaches of the Roper River (Cann, 1972). A list of current holdings in Australian Museums (AM, Australian Museum; QM, Queensland Museum; SAM, South Australian Museum; NTM, Northern Territory Museum), excluding those of Table 1, is as follows:

AM R40700, 08°55'S 143°03'E, Kuru [Village], Western District, PNG; AM R129346, Greta Creek, near Bowen; QM J5269, 18°04'S 146°33'E, Palm Is., NEQ; QM J10265, 20°24'S 148°35'E, Proserpine, NEQ; QM J13326, 19°16'S 146°49'E, Townsville, Thornley Pk, NEQ; QM J15560, J15900, 19°13'S 146°38'E, Townsville, Black R., NEQ; QM J20627/28/30/31/33/35, 14°35'S 144°03'E, Wakooka Outstation, lagoon 6.4km W, NEQ, 29 Nov, 1970; QM J36751, 15°25'S 141°58'E, Mitchell R., NWQ, late 1978; QM J37566, 14°07'S 143°16'E, Stewart R. 23km NNW Mt Croll NEQ, 6 Aug, 1979; QM J37819, 17°53'S 142°34'E, Cape York Peninsula, Gilbert R., NEQ, 10 Aug, 1979; QM J45005, 19°14'S 144°02'E, Lynd Hwy, NEQ, 1 Dec 1981; QM J47923, 180°39'S 146°01'E, Ingham Q, 19 Mar, 1988; QM J50730, 19°16'S 146°49'E, Townsville Town Common , NEQ, 2 Jul, 1990; QM J50731, J50732, J50997, J50998, 16°58'S 138°05'E, 5km SW of Old Doomadgee, NWQ, 24 Jun 1990; SAM R14361, 17°56'S 138°49'E, Doomadgee Mission, NWQ, Jun, 1963; NTM R5753 , 14°53'S 135°43'E, Maria Is., NT, 11 Jul, 1972; NTM R5898, 14°53'S 135°43'E, Maria Is., NT, 26 Jul, 1972.

Chelodina longicollis, *C. novaeguineae* and *C. steindachneri* are closely related. Their distributions (Fig. 1) suggest that their common ancestor may have had a distribution extending around much of the periphery of the Australian continent. This widespread species may have exhibited clinal variation in morphology and reproductive parameters consistent with differences we observe

FIG. 1. A map of Australia showing the locations of collection of specimens held in Australian museums (●) and the likely distribution of *Chelodina novaeguineae* in stipple. Shown also are the distributions of *C. longicollis* and *C. steindachneri* (after Cogger, 1988). The exact boundary between *C. longicollis* and *C. novaeguineae*, while in the Burdekin drainage (John Cann, pers. comm.), is uncertain.

in these characters among the three species today. Progressive aridity in the Pleistocene, around 25,000 years ago, or earlier during similar periods of expanding aridity in the past 15 million years may have led to the separation of three isolated populations, the one in the west speciating to *Chelodina steindachneri*, the one in the north and New Guinea speciating into *C. novaeguineae* and related forms and the one in the southeast speciating into *C. longicollis*. Studies of populations of *C. longicollis* and *C. novaeguineae* in the Burdekin drainage where they are in sympatry or parapatry with possible hybridization (John Cann, pers. comm.) are worthy of further investigation.

Chelodina novaeguineae occupies semi-permanent and seasonally ephemeral waterholes throughout its range and occurs sympatrically with *C. rugosa* in the Gulf country (Covacevich et al., 1990). Unlike *C. rugosa* in these waterholes, *C. novaeguineae* will migrate many kilometres overland to permanent water rather than aestivate (Covacevich et al., 1990; later expanded in pers. comm.). This seems to be a hazardous strategy in waterholes that dry annually. *C. novaeguineae* in the Daly Waters area, on the other hand, appear to aestivate and can be dug out of the mud when the waterhole dries up (Bill Cook, pers. comm.)

The presence of *C. novaeguineae* in the Roper River was known to Aboriginal people at Jinduckin near Mataranka, who hunt for 'Nganymalin', the 'smelly armpit turtle', in small creeks well upstream (Jesse Roberts, Mangarrayi language group, pers. comm.). A pungent secretion exuded from glands in the auxillary and inguinal pockets is a distinctive feature of *C. novaeguineae* and its southern relative, *C. longicollis*. Four other species of freshwater turtle also inhabit the Roper River, 'Jarnamanjarr' (*C. rugosa*), 'Gorronani' (*Elseya dentata*), 'Marndirrin' (*Emydura 'australis'*) and 'Jabada' (Jesse Roberts, pers. comm.). Jabada is described as a flat-headed short-necked turtle and may possibly be *Elseya latisternum*, although *E. latisternum* has not been officially recorded from the Roper. Interestingly, Aboriginal people at Jinduckin claim that, contrary to other reports (e.g. John Bywater, cited in Georges & Kennett, 1989), the Pig-Nosed Turtle (*Carettochelys insculpta*) does not occur in the Roper, the nearest place they caught them was in the Victoria River at Timber Creek. The distribution of *C. insculpta* may be more restricted in the Roper River than in other drainages where it is found.

The eggs and hatchlings of *C. novaeguineae* (this study; Grossman, 1988) are similar in size and appearance to those of *C. longicollis* (Vestjens, 1969; Kennett & Georges, 1990). The bright orange stripes on the plastron of hatchlings may be aposematic which, allied with their pungent secretion, may act as a deterrent to predators. The colouration fades with age (Cann, 1981) and may not be as marked in captive raised juveniles (Grossman, 1988).

Our gravid specimen and a gravid female collected by John Cann (10 August, 1979) from the Gilbert River on the Cape York Peninsula north east Queensland (QM J37819) indicate that nesting may occur throughout the tropical dry season, equivalent to the temperate autumn and winter. If our observed incubation period of 120 days approximates the natural incubation period, then hatching would occur in the late dry or early wet season, equivalent to the temperate spring and summer. These results are in conflict with the conclusions of Legler (1981, 1985) who describes *C. novaeguineae* as a temperate breeder, nesting in spring with hatching before autumn. Legler (1981, 1985) recognizes two groups within the genus *Chelodina* and characterizes the groups as exhibiting a tropical reproductive pattern and a temperate reproductive pattern. *C. novaeguineae* effectively straddles both groups, with the small

egg size of the temperate pattern and the nesting and long incubation period of the tropical pattern. These data suggest that the reproductive pattern of *C. novaeguineae* may have changed as it has moved north from its hypothesised evolution in southern Australia (Legler, 1981, 1985) and that phylogenetic conclusions based on reproductive patterns may be unsound.

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RE-EXAMINATION OF THE VENATION OF *OSMYLOPSYCHOPS SPILLERAE* TILLYARD FROM THE TRIASSIC OF QUEENSLAND

KEVIN J. LAMBKIN

Lambkin, K.J. 1992 06 29: Re-examination of the venation of *Osmylopsychops spillerae* Tillyard from the Triassic of Queensland. *Memoirs of the Queensland Museum* **32**(1): 183-188. Brisbane. ISSN 0079-8835.

The finding of new material has permitted re-examination of the venation of the Triassic neuropteran *Osmylopsychops spillerae* Tillyard. Many of the features of Tillyard's reconstruction of the forewing of the species are shown to be erroneous. □*Osmylopsychops spillerae, Neuroptera, Insecta, Triassic, Queensland.*

Kevin J. Lambkin, Honorary Research Fellow, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101; Correspondence to: 75 Alexandra St, Bardon, Queensland, Australia 4065; 22 November, 1991.

In the last of his 10 part series on the Mesozoic insects of Queensland, Tillyard (1923) described a broad-winged psychopsid-like lacewing from the Triassic of Denmark Hill in south-eastern Queensland (27°37'S, 152°47'E) as *Osmylopsychops spillerae* Tillyard. *Osmylopsychops* Tillyard was ascribed to the new family Osmylopsychopsidae by Martynova (1949) and, in 1953, Ellenberger et al. augmented the genus with their description of *O. radialis* from the Upper Triassic of France.

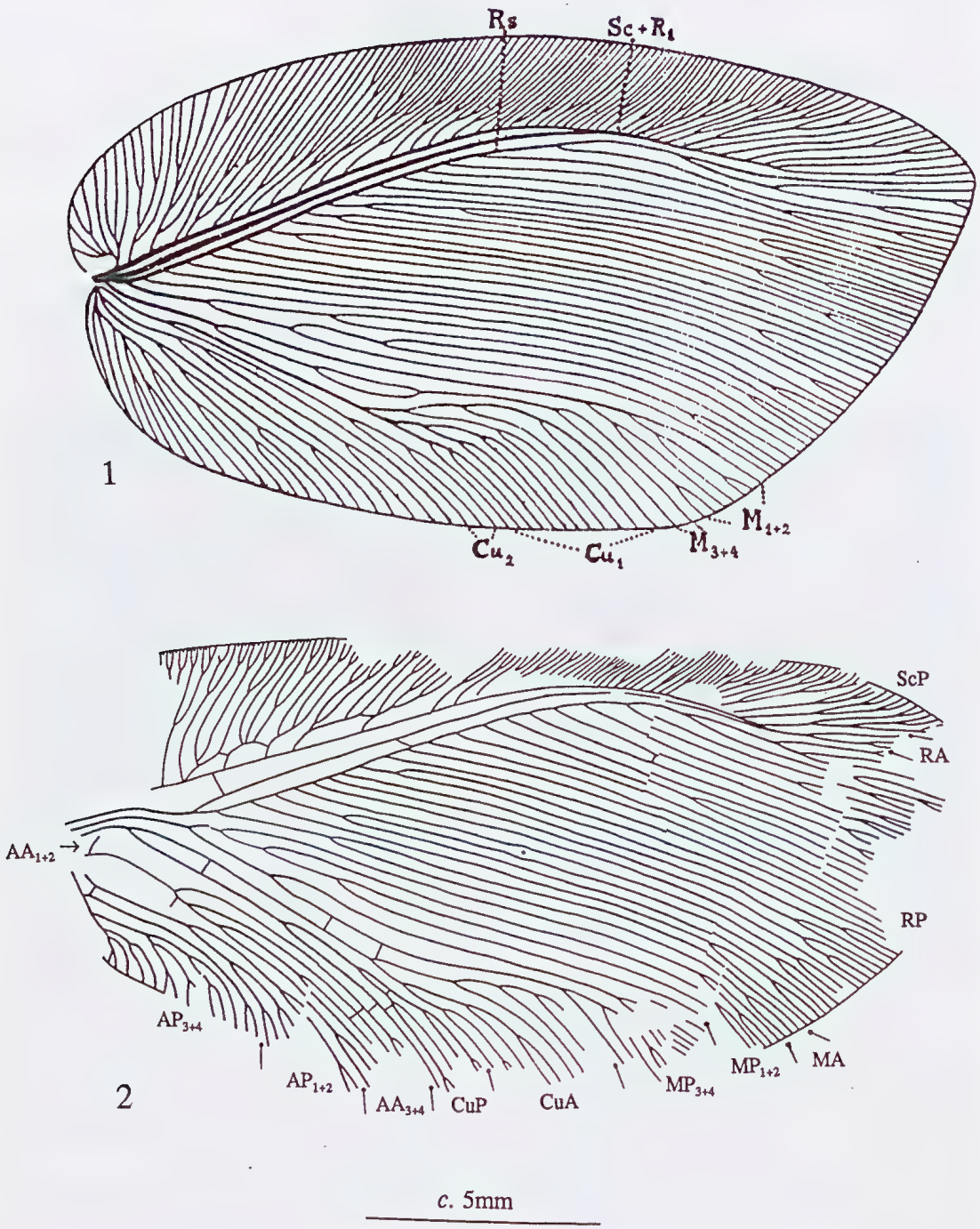
O. spillerae was based on two wing fragments (Tillyard, 1923, pl. XLIII, figs 39,40), from which Tillyard 'reconstructed' the forewing venation (Fig.1). Because of the fragmentary nature of this type material (Figs3,4), much of the reconstruction was notional and, as often happens with such 'best guess' reconstructions, its publication and subsequent reproduction (e.g. Riek, 1970) entrenched in the literature an assumed to be accurate 'complete' venational scheme that became a baseline for subsequent comparisons with similar species.

The purpose of the present work is to provide a more accurate view of the venation of *O. spillerae* and in so doing to exclude Tillyard's reconstruction, visually appealing though it may be, from the data set of fossil Neuroptera. The re-examination of the venation of the species has been made possible by the collection in more recent years of several specimens of *O. spillerae* from the Triassic of Mount Crosby in south-eastern Queensland (27°32'S, 152°48'E), from where the species was first recorded by Riek (1955). Examination of this new material as well as of Tillyard's original Denmark Hill specimens provides an almost complete picture of the forewing venation of the species (see Fig.2).

Tillyard's material was collected in grey shales of the Blackstone Formation that were exposed in a small quarry at Denmark Hill, a suburb of the town of Ipswich (Dunstan, 1916). Mount Crosby fossil insects occur in green shales of the Mount Crosby Formation and have been collected at five separate exposures designated as Fossil Insect Localities A, B, C, D and E (details in Allen, 1961). Both Formations are Late Triassic (Karnian) and form part of the Ipswich Coal Measures, with the Mount Crosby Formation lower in the sequence (Cranfield et al., 1976).

With one exception, the determination of whether the isolated wing fragments described herein are of fore- or hindwings has not been possible. The closest living species for comparative purposes is the psychopsid *Megapsychops illidgei* (Froggatt). In this species the basic venational patterns of the fore- and hindwings are very similar (see Tillyard, 1919, pl. LXXVII, fig.4; New, 1988, figs196,197) and, because of this similarity, I believe it is valid, for the sake of convenience of discussion, to regard all wing fragments of *O. spillerae* considered herein as probable forewings. The exception to this uncertainty is specimen UQDE CB14 (Fig.6). It has the proximal regions of AA_{3+4} and AP widely separated and the stem of AA_{1+2} clearly developed (both forewing characters of *M. illidgei* and other living psychopsids), and is therefore almost certainly a forewing.

The venational terminology used herein is that of Kukalová-Peck (1983, 1991; see also Lawrence et al., 1991). The following museum abbreviations apply: GSQ, Geological Survey of Queensland; QM, Queensland Museum; UQDE, University of Queensland, Department of Entomology.



FIGS 1,2. *Osmylopsychops spillerae*. 1, Tillyard's reconstruction (1923, text fig.93). 2, Composite of QM F18921 (Fig.5), UQDE CB14 (Fig.6), QM F18922 (Fig.7), and part of GSQ 283a (Fig.4) (proximal sections of ScP, RA, RP, CuA (thicker veins) not drawn to scale).

MATERIAL EXAMINED

Holotype GSQ 314 (central region of ?forewing), 'Osmylopsychops / ~~reevei~~ spillerae Till. / Holotype / Denmark Hill / Ipswich', '3149.9'; Heautotype [= autotype] GSQ 283a (apical $^2/_3$ of ?forewing), 'G', 'Osmylopsychops / ~~reevei~~ spillerae Till. / Heautotype / Denmark Hill / Ipswich / Trias.'; QM F18921 (central region of ?forewing), Mount Crosby Fossil Insect Locality D (collected by K J Lambkin, 20.viii.1972); UQDE CB14 (base of forewing), Mount Crosby Fossil Insect Locality B; QM F18922 (apex of ?forewing), 'L114 Mt Crosby shale / (910805-911805 Ipswich / 1 mile military map - upper bed) / 10.vii.1969 / E. Dahms', [Mount Crosby Fossil Insect Locality C]; QM F18923 (?forewing fragment), Mount Crosby Fossil Insect Locality B (collected by K J Lambkin, 24.viii.1974).

DESCRIPTION OF FOREWING VENATION (Figs 2-8)

Broad wing of psychopsid type, length c. 18.5mm (Fig.2); costal space quite broad basally, tapering apically (Figs4,5); costal crossveins irregular, mostly deeply forked and extensively branched, almost upright basally, becoming gradually more inclined apically, more closely spaced in 'pterostigmal' area, with a limited series of interconnecting crossveins basally just above ScP (Figs3-7); ScP converging and either ?fused or ?connected by a very short crossvein with RA apically (Figs4,7), entering margin before wing apex; 1 upright scp-ra just beyond radial fork (Figs5,6); ScP, RA and stem of RP curved apically (Fig.2), 1 inclined ra-rp at c. midlength (Fig.5); RP with at least 18 pectinate branches, a few of these forked basally or c. midlength, all with apical branches (Figs4,5,7,8); crossveins of RP field apparently few in number, only 1 or 4 detected (Figs 5,8); MA simple or deeply forked (Figs3,5,6,8); MP occupying a large central area of the wing, its primary forking very close to the base (before that of R - Fig.6), with 6 or 7 branches at midlength (Figs3,5,6), and extensively dichotomously forked apically (Figs5,7); MP_{1+2} dichotomous in holotype, but in some specimens tending to pectination, in UQDE CB14 this pectination mirroring that of RP (Fig.6); MP_{3+4} forking a little later than MP_{1+2} (Figs3,6,8), MP_4 of holotype with an enclosed cell at c. midlength (Fig.3); medial, cubital and anal fields with a few randomly placed crossveins as illustrated in Figs3,5,6,8 (possibly preservation dependent); CuA extensively dichotomously forked from c.$^2/_3$ length with branches curved anteriorly (Figs3,5); CuP occupying only a narrow area of the wing, more deeply dichotomously forked than CuA, CuP1 more deeply forked than CuP_2 (Figs3,5,6); AA_{1+2} developed as a short spur directed obliquely towards Cu (Fig.6); AA_{3+4} extensively dichotomously forked from c.$^1/_4$ length (Fig.6); AP1+2 dichotomously forked from c.$^1/_2$ length, less extensive than AA_{3+4} or AP_{3+4} (Fig.6); AP_3 joined to AP_2 by a short crossvein basally, simple for almost entire length, with 2 small branches apically (Fig.6); AP_4 extensive, occupying as much of the margin as AP_1, AP_2 and AP_3 combined, extensively dichotomously forked with branches directed apically (Fig.6); trichosors present, at least along fore margin (Figs5,6); 1 nygma detected, placed centrally between 2nd and 3rd branches of RP (Fig.5).

NOTES

Figure 2 is a composite of UQDE CB14 (Fig.6), QM F18921 (Fig.5), QM F18922 (Fig.7), as well as a small part of GSQ 283a (Fig.4) ('pterostigmal' region only). It illustrates the known features of the presumed forewing of *O. spillerae*. The major differences between this composite and Tillyard's reconstruction (Fig.1) are listed below. Certain features, such as the wing shape and the venation of the humeral region and parts of the fore, apical and hind margins, are not preserved in the material examined and remain unknown.

1. Structure of MP (= M of Tillyard's notation)

Because Tillyard's specimens did not show the important basal structures of the main veins (as now provided by UQDE CB14 - Fig.6), he conjectured that MP was of minor extent with its primary forking well beyond that of R (as is apparently the case in recent psychopsids). The new material indicates that MP forks very early (before the primary radial fork), is multibranched, and occupies a large central area of the wing. The veins shown by Tillyard as the first two branches of RP (Rs of his notation) are indeed part of MP.

The structure of MP in *O. spillerae* is especially interesting in providing a clue to the homology of 'MP' in the wings of living species of the Psychopsidae. In the forewing of these species there is a variably developed weak posterior branch leaving MP before the primary forking of R, in exactly the same position as MP_{3+4} in *O. spillerae*. In larger species (e.g. *M. illidgei*,

FIGS 3-8. *Osmylopsychops spillerae* (proximal sections of ScP, RA, RP, CuA (thicker veins) not drawn to scale). 3, GSQ 314 (holotype). 4, GSQ 283a ('heautotype'). 5, QM F18921. 6, UQDE CB14. 7, QM F18922. 8, QM F18923.

Psychopsis barnardi Tillyard) this branch exists as a very weak vein which peters out after running for a short distance along a fairly deep furrow in the membrane. In species of smaller size the furrow and a kink in the stem at the point of forking (e.g. *P. insolens* McLachlan), or simply the suggestion of a fold in the membrane (e.g. *P. coelivagus* (Walker)), is all that remains. Based on the structure of MP in *O. spillerae*, the much reduced extreme basal posterior branch of MP described above is the remnant of MP_{3+4} and the vein system usually labelled as 'MP' in living psychopsids is MP_{1+2} only.

2. Structure of Cu

In Tillyard's reconstruction the primary forking of Cu is a considerable distance from the base, and CuP forks at the same level as CuA and has only three branches. Specimen UQDE CB14 (Fig.6) shows that the primary fork of Cu is placed extreme basally (as occurs in the Psychopsidae and most Neuroptera), and that CuP forks much earlier than CuA and has at least six major branches.

3. Structure of A

The anal area in Tillyard's reconstruction is almost entirely conjectural and bears only marginal resemblance to that described herein (see especially Fig.6). The new information shows that the basal sections of Cu→CuP, AA_{3+4} and AP_{1+2} are much more widely spaced than in Tillyard's reconstruction; the basal section of AA_{3+4} is curved anteriorly, not posteriorly; AA_{3+4} and AP_{1+2} are not fused at the base; and AP_{3+4} is smaller in area and has fewer major branches which are directed apically rather than posteriorly.

4. Primary forking of R

Tillyard's reconstruction shows the primary forking of R very close to the base of the wing. UQDE CB14 (Fig.6) shows that R forks much further distally than this, well beyond the primary forkings of Cu and AA_{3+4}.

5. Marginal end-twigging of veins

End-twigging of veins is much more pronounced along the fore and hind margins (see Fig.2) than indicated by Tillyard.

6. Wing proportions

Comparison of Figures 1 and 2 indicates that the presumed forewing of *O. spillerae* is not as broad as suggested by Tillyard.

The relationships of *O. spillerae* (and *O. radialis* which, based on the figure of Ellenberger et al. (1953, fig.1), appears to be congeneric) remain problematical. *Osmylopsychops* is just one of a large number of diverse Mesozoic psychopsid-like wings (see Martynova, 1949, and numerous subsequent descriptions of additional species) that, as a group, requires critical re-examination and reappraisal. What can be said at this stage, however, is that *Osmylopsychops* does not possess the set of apomorphic wing features characteristic of the Psychopsidae (viz ScP, RA and stem of RP evenly spaced and braced by numerous crossveins; MP_{3+4} much reduced; CuA and CuP strongly posteriorly pectinate; crossveins mostly aligned into two or three gradate series) and is thus not attributable to that family (see also Riek, 1955).

ACKNOWLEDGEMENT

I am grateful for the assistance of Susan Parfrey of the Queensland Department of Resource Industries who arranged the loan of Tillyard's types.

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NOTES ON *SPONDYLUS* LINNAEUS WITH DESCRIPTIONS OF TWO NEW SPECIES FROM WESTERN AUSTRALIA (MOLLUSCA: BIVALVIA: SPONDYLIDAE)

KEVIN LAMPRELL

Lamprell, K. 1992 06 29: Notes on *Spondylus* Linnaeus with descriptions of two new species from Western Australia (Mollusca: Bivalvia: Spondylidae). *Memoirs of the Queensland Museum* 32(1): 189-194. Brisbane. ISSN 0079-8835.

Two new species of Spondylidae, *Spondylus clarksoni* sp.nov. and *S. eastae* sp.nov., are described from Western Australia. Additional taxonomic notes are presented on other Recent *Spondylidae*. *Spondylus asperrimus* Sowerby, 1847 is elevated to specific rank; *S. butleri* Reeve, 1856 is removed from the synonymy of *S. longitudinalis*; *S. erinaceus* Reeve, 1856 is relegated to the synonymy of *S. gilvus* Reeve, 1856; *S. pratti* Parth, 1990 is placed in the synonymy of *S. pictorum* Schreibers, 1793; a reliable locality is established for *S. gravis* Fulton, 1915; *S. raoulensis* Oliver, 1915 (July) is given priority over *S. iredalei* Fulton, 1915 (October); and *S. prionifer* Iredale, 1931 is redescribed. □*Mollusca, Bivalvia, Spondylidae, Spondylus, new species, taxonomy, Western Australia.*

Kevin Lamprell, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 3 February, 1992.

Since publication of *Spondylus: Spiny Oyster Shells of the World* (Lamprell, 1987), I have studied type specimens in overseas museums and a range of new material from the Australian region. Two undescribed species of *Spondylus* from Western Australia were recognised and taxonomic information on several previously described species was updated.

Abbreviations used in text: AM = Australian Museum; QM = Queensland Museum; WAM = Western Australian Museum; MV = Museum of Victoria; pv = paired valves.

SYSTEMATICS

Family SPONDYLIDAE Gray, 1826
Spondylus Linnaeus, 1758

Spondylus clarksoni sp.nov.
(Fig. 1a-d)

ETYMOLOGY

For Mr Peter Clarkson who donated specimens for study.

MATERIAL EXAMINED

HOLOTYPE: WAM562-91, 1 pv, exposed on dead coral faces, 9-13m, Bennett Shoal, central Exmouth Gulf, W.A., 1991, P. Clarkson. Height 100mm, length 86mm, width 48mm.

PARATYPES: AMC167693, MVF6552, QMMO32909, 3 pv, exposed on sponge covered limestone reef in tide rip, 15-22m, S end South Muiron I., Exmouth Gulf, W.A., 1991, P. Clarkson.

OTHER MATERIAL: Four specimens from Pt Lefroy, southern end Exmouth Gulf, north W.A., P. Clarkson.

DIAGNOSIS

Shell pecten-shaped, slightly oblique, solid. Hinge typical for the genus. Top (left) valve moderately convex, more so umbonally; internally, slightly excavated under the hinge plate with a strong, wide, crenulated margin; hinge-line moderately wide. Sculpture of five, strong, rounded, principal radial ribs ornamented by strong, upright, spatulate spines which are channelled on the underside, narrow and strong at their bases, wide and flattened at their tips. Rib interstices with five to twelve minor radial ribs, central longer and stronger ornamented with dense, sharp, overlapping spines, and whose interstices contain smaller ribs which are ornamented with even smaller and finer spines or nodules. Lower (right) valve equally as convex as the top valve; cardinal area triangular and moderately deep; internally, moderately deep under the hinge plate with a strong, wide, crenulated margin. Sculpture (where not affixed) of thin concentric foliations with few, irregularly placed, strong spines. Area of attachment varying from 50-100% of the lower surface. Colouration pure white with pink-rose umbonally extending approximately one-third down the shell surface. Height 70-100mm, length 70-87mm, width 38-54mm.

HABITAT AND DISTRIBUTION

Covered in red sponge attached to low-profile limestone reefs, on a sandy bottom, among spon-

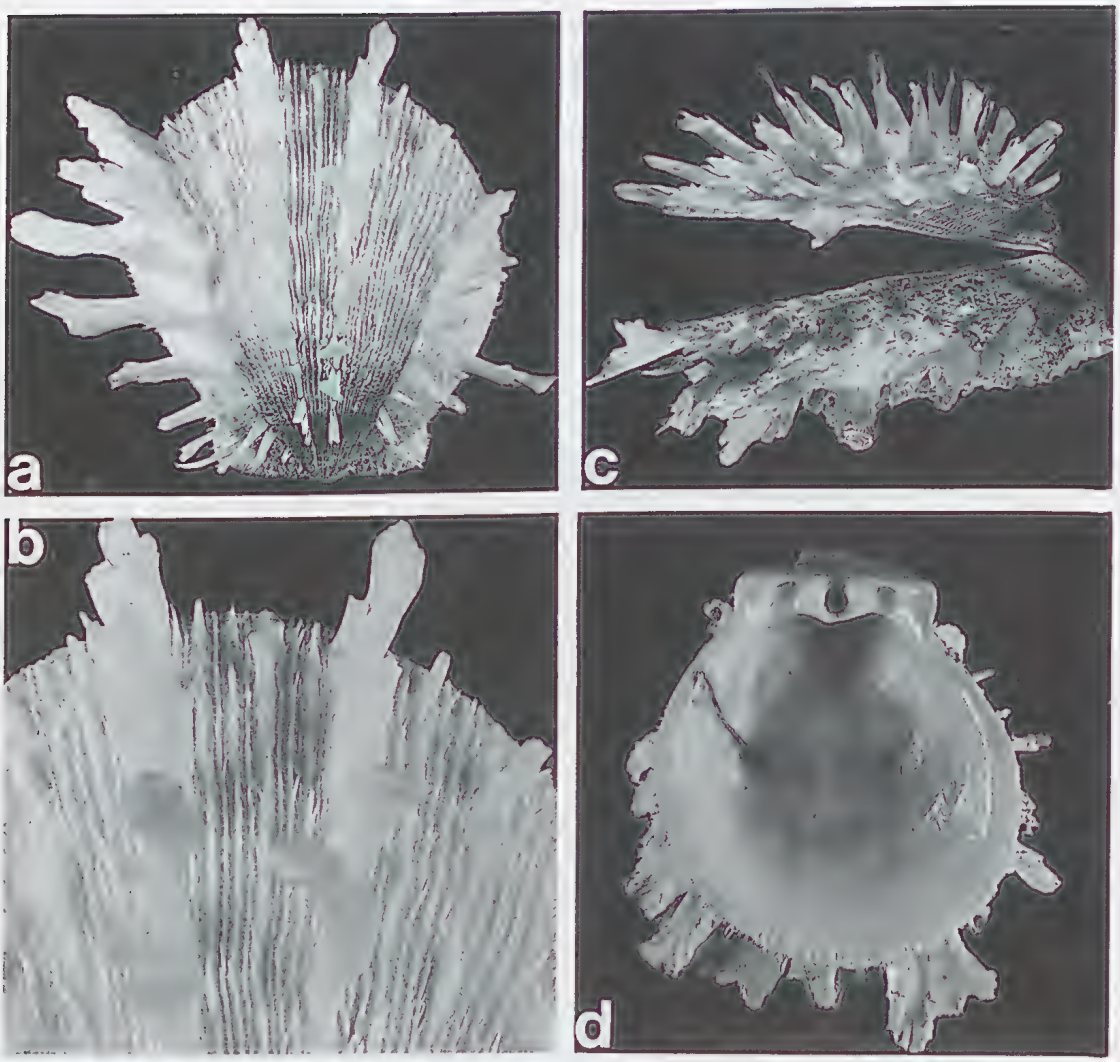

FIG. 1. *Spondylus clarksoni* sp.nov. a-d, Bennett Shoal, central Exmouth Gulf, Western Australia. WAM562-91, holotype. a, top valve. b, sculpture on top valve. c, side view. d, interior of lower valve.

ges and gorgonian corals. Apparently restricted to north Western Australia (Shark Bay to Broome).

REMARKS

Compared with *Spondylus clarksoni*, *S. sinensis* Schreibers, 1793 has fewer, stronger, interstitial ribs devoid of ornamentation, strong principal ribs on the lower valve (absent in *S. clarksoni*) and a very small attachment area. *Spondylus victoriae* Sowerby, 1843, which occurs sympatrically, has long, sharp to spatulate principal spines on both valves and fewer, stronger interstitial spines. Compared with *S. tenellus* Reeve, 1856, which occurs in southern Australia, *S. clarksoni* is larger and heavier, has stronger ribs, wide, spatulate spines and weaker interstitial spining. The spining and ribs in both valves of *S. tenellus* are always orange or pink whereas those of *S. clarksoni* are white.

Spondylus eastae sp.nov.
(Fig. 2a-d)

ETYMOLOGY

For Aileen East who has donated material for study.

MATERIAL EXAMINED

HOLOTYPE: WAM563-91, 1 pv, 7-11m, Schofield Shoal, SW Exmouth Gulf, W.A., 1991, P. Clarkson. Height 82mm, length 64mm, width 37mm.

PARATYPES: QM MO32910, AM C167694, MV F6553, 3 pv, exposed on sponge covered limestone reef

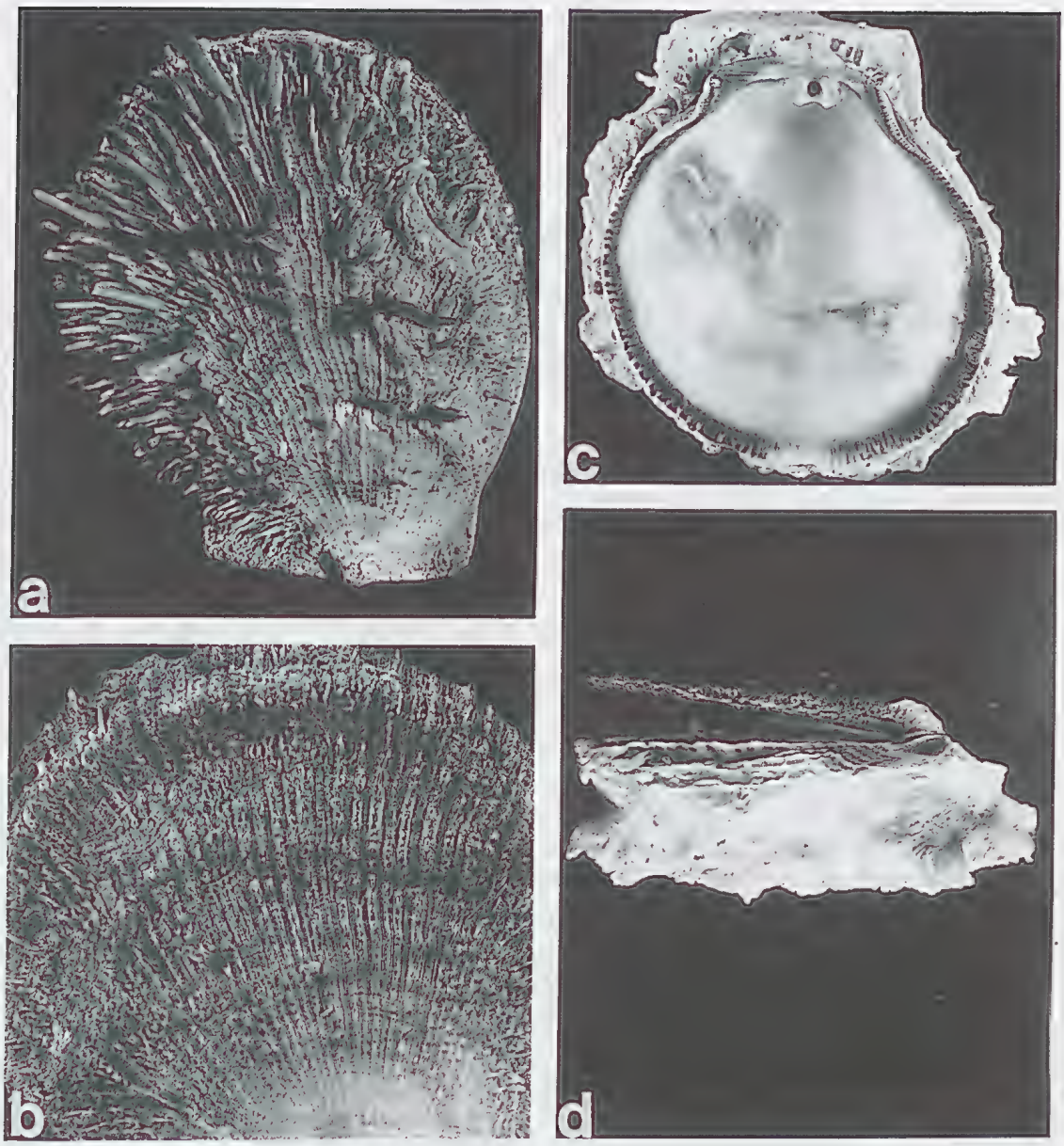

FIG. 2. *Spondylus eastae* sp.nov. a. Schofield Shoal, South West Exmouth Gulf, Western Australia. WAM563-91, holotype. b-d, Muiron I., Exmouth Gulf, Western Australia, paratype. a, top valve. b, sculpture of top valve. c, interior of lower valve. d, side view.

in tide rip, 15-22m, S end South Muiron I., Exmouth Gulf, W.A., 1991, P. Clarkson.

OTHER MATERIAL: Cape Keraudren, W.A., attached to rock at low tide, Sept. 1987, K. Lamprell; Port Hedland, W.A., attached to coral, low tide, Sept. 1987, K. Lamprell; Exmouth Gulf, Town Beach, 6m, attached to rocks, Sept. 1987, K. Lamprell and P. Spoor; Cape Keraudren, W.A., Sept. 1982, L. Marrow.

DIAGNOSIS

Shell ovate to pear-shaped; solid. Hinge typical for the genus. Top (left) valve moderately convex umbonally, remainder of surface depressed to moderately concave; internally smooth, slightly excavated under the hinge plate, with a strong, wide, moderately crenulated margin; sculpture of numerous, weak radial ribs, ornamented by short,

dense, strong, depressed, sharp spines and a few longer, irregular, flat, spatulate spines which are stronger at their bases. Rib interstices with a few irregular, obsolete radial ridges which are ornamented with dense, nodules or small spines. Lower (right) valve convex, moderately shallow to deep; cardinal area narrowly triangular, shallow; internally moderately excavate with wide, moderately crenulated margin; sculpture (where not affixed) of thin concentric foliations covering most of the surface, or otherwise with similar ribs and ornamentation to upper valve. Area of attachment varying from 10-70% of lower surface. Colouration typically brown/maroon to brick- red, orange or purple; umbones white with small flecks of brown; lower valve with similar colouration to top valve; internally blue-white centrally with deep purple-brown, red or orange margins and a dark brown margin towards the hinge. Height 72-93mm, length 57-79mm, width 30-42mm.

HABITAT AND DISTRIBUTION

Embedded in dead coral boulders and depressions on reef, among sponges and gorgonian corals; usually covered in red sponge. Restricted to north Western Australia.

REMARKS

Compared with *Spondylus eastae*, *S. barbatus* Reeve, 1856 has five or six strong, principal ribs with alternating, dense, sharp and spatulate spines, and colour bars or bands at the auricles. *Spondylus violascens* Lamarck, 1819 has been confused with *S. eastae* but has much stronger and denser spining on both valves, much less affixation and spatulate spines which are hollow rather than flat. The north-west Australian distribution given by Lamprell (1987) for *S. violascens* represents the range of *S. eastae*. *Spondylus multimuricatus* Reeve, 1856 is similar in shape and size to *S. eastae* but has stronger radial ribs ornamented with hollow, blunted spines (not spatulate) and with interstices that have few, irregular, smaller stout spines.

ADDITIONAL NOTES

Spondylus asperrimus Sowerby, 1847

REMARKS

Lamprell (1987: pl.3, fig. 1a-c) considered this species to be a form of *S. linguafelis* Sowerby, 1847. However it can be separated from that species by its more elongate shape, shorter spines and rows of fine nodulose spines in the interstices. It is usually affixed by almost the entire lower valve (or surface) whereas *S. linguafelis* is usually affixed by the cardinal area.

DISTRIBUTION

Philippines, north Western Australia and central Queensland coastal areas.

Spondylus butleri Reeve, 1856

REMARKS

Lamprell (1987: pl.4, fig. 2a-c) considered *S. longitudinalis* Lamarck, 1819 to be a prior name for the more widely used *S. butleri*. The type of *S. longitudinalis* (Museum of Natural History, Geneva) was examined and considered to be the same as *S. zonalis* Lamarck, 1819. Another specimen figured and referred to by Chenu (1845: pl.9, fig 2-2a) as *S. longitudinalis* (but not marked as a type), was even more similar to the type of *S. zonalis* . Fulton (1915:360, species 86) remarked, 'I have received a photograph of the shell figured by Chenu (*S. longitudinalis*), which is now in the Geneva Museum; the authorities there cannot say with any certainty that it is the actual type specimen'. *Spondylus butleri* should be used for the species figured in Lamprell (1987: pl.4, fig 2a-c).

DISTRIBUTION

Philippines, Madagascar, Micronesia and the Great Barrier Reef, Queensland.

Spondylus gilvus Reeve, 1856

S. erinaceus Reeve, 1856.

REMARKS

Although figured separately by Lamprell (1987: pl. 17, fig. 2a, b; pl. 17, fig. 1), types (British Museum Natural History) of *S. gilvus* and *S. erinaceus* revealed insufficient variation to maintain their separation.

Spondylus pictorum Schreibers, 1793

S. crassisquamatus Lamarck, 1819.
S. pratti Parth, 1990.

REMARKS

Three specimens of *S. pratti* from the type locality (Somalia) were compared with *S. pictorum*. Two were very mature but retained most of their sculpture; the third was younger with full sculpture. In describing *S. pratti*, Parth referred to

the two valves as unequal, the top valve larger and more gibbose. In all specimens examined, each valve was equally convex and gibbose. Parth also referred to both valves of *S. pratti* as equally sculptured with six principal ribs. In two of the specimens the top valve had six principal ribs while in the lower valve, one specimen had six and the other seven principal ribs.

While Parth (1990:6) only compared *S. pratti* with *S. americanus* 'because of its large size', numerous other *Spondylus* are equally as large or larger than this species: in particular, *S. pictorum* Schreibers, 1793 (Lamprell, 1987: pl. 23, fig. 1a-d), which shares a similar distribution to *S. pratti*, viz Somalia. *Spondylus pictorum* is equally as convex as *S. pratti*, has similar sculpture, rib count, interstitial sculpture and spining; and both have stout, upright principal spines that are channelled beneath, extending the full length of the spine. Colouration in specimens examined was similar to *S. pictorum*: white in base colour with bands of pink, red or brown and pink in the umbonal area. The juvenile specimen had white in the interstices and pink spines whereas, in some specimens of *S. pictorum*, the interstices are white and red or orange-brown. I am unable to find any features, apart from this interstitial colour variation, to separate *S. pratti* from *S. pictorum*.

Spondylus gravis Fulton, 1915

REMARKS

The type is in the British Museum (Natural History) without a specified locality. Recent trawling of several specimens (Lamprell, 1987: pl. 28, fig. 1) in 200-300m off Capo Ras Hafun, Somalia, gives reliable locality data.

Spondylus raoulensis Oliver, 1915

S. iredalei Fulton, 1915.

REMARKS

Lamprell (1987: pl. 29, fig. 4) incorrectly listed this species as *S. iredalei.* Fulton's work was published in two parts and the section naming *S. iredalei* was included in the second part printed in October 1915. The description of *S. raoulensis* by Oliver was published on the 12 July 1915 and thus has priority over *S. iredalei.*

Spondylus prionifer Iredale, 1931

REMARKS

Lamprell (1987: pl.25, fig.1) incorrectly listed *Spondylus prionifer* as a synonym of *S. tenellus* Reeve, 1856. The holotype (Australian Museum, Sydney) is immature and superficially similar to *S. tenellus*. However, numerous specimens recently collected on the Gneering Shoals, Mooloolooba, south Queensland, differed from *S. tenellus*. On the basis of this material, a more detailed description of *S. prionifer* follows. The species was figured by Lamprell (1987: pl. 25, fig. 3b; pl. 30, figs 1, 2).

DESCRIPTION

Shell height to 85mm, width to 65mm and depth of conjoined valves to 45mm, pecten-shaped. Top (left) valve slightly convex to depressed; lower (right) valve moderately deep, cup-like, cardinal area trigonal, moderately extended; internally with the margins strongly crenulated; area under the lunule and hinge plate, deep and extended; sculpture of both valves with 35-40 strong radial ribs with weaker intermediate ribs in the interstices; ribs ornamented with numerous depressed or hooked spines which vary from sharp to spatulate, stronger marginally and with a longitudinal furrow beneath and finely denticulate edges; interstitial ribs with two or three rows of fine spines or striae. Area of attachment of the lower valve variable but usually restricted to the umbonal area. Colouration variable, usually white with concentric bands of red and white ribs marginally, rarely all orange or red-brown; internally blue-white with margin crenulations variegated white and red or orange.

HABITAT AND DISTRIBUTION

Attached to corals or rock to 33m. Central Queensland (Capricorn Channel), south Queensland (Gneering Shoals) and Sydney Harbour, N.S.W.

ACKNOWLEDGEMENTS

Thanks are due to the Curators and staff of the British Museum (Natural History), Museum National d'Histoire Naturelle, Paris and the Museum of Natural History, Geneva for their assistance in examining essential study material; to Dr John Stanisic, Queensland Museum and Dr John Healy, Queensland University for critically reading the manuscript and for advice on manuscript preparation; to Mr Ian Loch, Australian Museum, for his research on *Spondylus iredalei/raoulensis*; and to Mr Luigi Bozzetti, Italy, for the loan of specimens.

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Fund. Overseas photographic expenses were partially met by funds received from the Keith Sutherland Award, Australian Museum, Sydney.

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THE SUBTRIBE HICKSBEACHIINAE (PROTEACEAE) IN THE AUSTRALIAN TERTIARY

ANDREW C. ROZEFELDS

Rozefelds, A.C. 1992 06 29: The subtribe Hicksbeachiinae (Proteaceae) in the Australian Tertiary. *Memoirs of the Queensland Museum* 32(1): 195-202. Brisbane. ISSN 0079-8835.

Wilkinsonia bilaminata F. Muell., a fossil fruit from deep leads at Gulgong, New South Wales is similar to fruits of extant genera *Athertonia* and *Heliciopsis* (subtribe Hicksbeachiinae: Proteaceae). *Athertonioides* Rozefelds is considered a synonym of *Wilkinsonia*. Fossil evidence of *Wilkinsonia* in the mid-Tertiary demonstrates that the subtribe was more widespread than at present. *Wilkinsonia* is more closely related to *Athertonia*, the north Queensland rainforest endemic, than to the South East Asian genus *Heliciopsis*.□ *Proteaceae, Hicksbeachiinae, Athertonia, Heliciopsis, Wilkinsonia, Athertonioides, fossil fruit, Australia, Tertiary.*

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Mueller (1879, 1883) described *Wilkinsonia bilaminata* on the basis of woody fruits from deep leads (buried placer deposits) below basalts in the Orange and Gulgong gold mining areas of New South Wales. Mueller (1879, 1883) recorded *W. bilaminata* from Beneree, near Orange at a depth of about 110-130ft and in deep leads at Gulgong at a depth of 140-175ft (Fig. 1). He was unsure of the affinities of *W. bilaminata* but suggested (1879: 170) that it 'may perhaps have belonged to the order of Sapindaceae; but with the material at present available it is impossible to find its exact ordinal position, as no external resemblance indicates any close relationship to existing genera'. The only surviving specimen located is in the Museum of Victoria (NMVP53092) from the Gulgong locality in New South Wales.

Palynological studies of the Home Rule Kaolin Deposit which is part of one of the deep leads in the Gulgong area indicates they are of late early to middle Miocene age (McMinn, 1981). Potassium-Argon dates of 14.8 ± 1.2 and 13.8 ± 1.1my BP. for basalts that overlie deep leads in this area (Dulhunty, 1971) indicate a minimum mid-Miocene age for this flora.

Fruits from the Oligocene Glencoe locality in central Queensland were placed in a new form genus *Athertonioides* which closely resembles those of the north Queensland endemic *Athertonia*, and South East Asian genus *Heliciopsis*, (both in subtribe Hicksbeachiinae) (Rozefelds, 1990a). Re-examination of topotypic material of *W. bilaminata* F. Muell. from the Gulgong locality also suggests inclusion in Hicksbeachiinae (Fig. 2).

In this paper *W. bilaminata* is redescribed and it's affinities discussed. The status of *Athertonioides* Rozefelds is also re-examined. Fruit anatomy of extant genera *Heliciopsis, Athertonia* and *Hicksbeachia* is also figured and the fossil record of Hicksbeachiinae in Australia is reviewed.

METHODS AND MATERIALS

To permit comparison with the fossil material, the soft outer exocarp and mesocarp layers of modern fruits were removed. Persistent fibres attached to the stony layer (endocarp) of the fruit were removed with a nylon brush. The endocarp was sectioned with a coping saw and the transverse sections polished with 1200 grit 'wet and dry sandpapers'. The sections were photographed with a Carl Zeiss DRC Stereo Microscope with MC63 camera attachment. Comparative modern Australian material figured in this paper will be donated to the Queensland Herbarium (BRI).

The term endocarp is used here in a descriptive sense and follows that of Sleumer (1955a,b), (Smith & Haas, 1975) and Filla (1926). Johnson & Briggs (1975), however, have concluded that this inner stony layer is part of the mesocarp. The mesocarp consisting of an outer zone of parenchymatous tissue with radial fibres and inner dense hard zone of tangentially oriented fibres.

Silicified fossil material from Glencoe (Queensland Museum locality QML511) is preserved as moulds with little or no internal cellular preservation. Gulgong and other deep leads fruits approach fusanites in appearance, which

suggests they have been subjected to considerable heat and pressure. During fossilization, the more volatile endocarp wall constituents are lost, leaving only the ligneous structure of the fruit. In modern fruits the volatile endocarp wall constituents are still present making comparisons difficult.

SYSTEMATIC PALAEOBOTANY

Family PROTEACEAE
Tribe MACADAMIEAE
Subtribe HICKSBEACHIINAE

Rozefelds (1990a) erected *Athertonioides glencoensis* for fossil fruits collected from the Glencoe locality in central Queensland. Re-examination of *Wilkinsonia bilaminata* also indicates close affinities with *Athertonia*. It is not warranted to maintain two form genera for fossil *Athertonia*-like fruits and so *Athertonioides* is here reduced to a synonym of *Wilkinsonia*. In his diagnosis of *Wilkinsonia*, Mueller (1879, 1883) drew prominent attention to the flattened nature of the endocarp and the ridging which are features, that are in part, due to compression during fossilization. An emended diagnosis of *Wilkinsonia bilaminata* is provided. The original specimen figured by Mueller (1879: pl. 3, fig. 4a,b) has not been located in the Museum of Victoria, Geological Survey of New South Wales or Australian Museum collections. It seems likely that as the original material was obtained by C.S. Wilkinson (Geological Survey, New South Wales), the figured specimen would have been lodged in their collections, but may have been subsequently lost in the Garden Palace fire, Sydney, 1882 (J. Pickett, pers comm. 1992). A neotype is erected here, which is probably the specimen figured by Mueller (1883: pl. 3).

Geological Survey of New South Wales specimens (MMF31337-31343) from the Newstead Mine, Elsmore, northern NSW have been tentatively compared with *Wilkinsonia* (Pickett et al., 1990). These compressed fruits however lack the reticulate lacunose ornamentation and longitudinal ridges characteristic of this genus. The affinities of these fruits remain unknown.

Wilkinsonia (F. Muell., 1879) emend.

TYPE SPECIES

Wilkinsonia bilaminata F. Muell., 1879.

FIG. 1. Localities mentioned in text and distribution of modern genera and species of Australian Hicksbeachiinae.

EMENDED DIAGNOSIS

Endocarp indehiscent, variable in shape and size, with variable development of longitudinal ridges, reticulate lacunose surface consisting of irregular depressions. Depressions variable in size. Base of depressions confluent with internal wall of endocarp. Incipient curved longitudinal ridge continuous from apex to base of endocarp. Irregular rows of small depressions between incipient ridge and edge of endocarp. Monolocular.

FIG. 2. Reproduction of Mueller's (1883) original figure of *Wilkinsonia bilaminata*, × 0.7. The specimens were originally illustrated by Mueller at natural size.

Wilkinsonia bilaminata (F. Muell., 1879) emend. (Figs 2, 3A-D).

1879. *Wilkinsonia bilaminata* F. Muell., p. 170, pl. 3, fig. 4a,b.
1883. *Wilkinsonia bilaminata* F. Muell., p. 7, pl. 3 (refigured herein).

MATERIAL EXAMINED

NEOTYPE: NMVP53092 (here designated), Black Lead, 140-170ft below basalt, Gulgong, NSW (Fig. 3A-D).

EMENDED DIAGNOSIS

Large round monolocular endocarp, with reticulate lacunose ornamentation consisting of longitudinal ridges with ramifying supporting lateral ridges. Approximate size of endocarp (due to fraying of edges), length 46.3mm, width 45.9mm. A prominent incipient lateral ridge extends from the apex to the base of the endocarp. A broad lateral field occurs between incipient ridge and edge of endocarp with minor accessory lateral ridges and irregular rows of small depressions. Endocarp thinly elliptical in lateral view, although this is due to lateral compression. Multiple irregular rows of depressions and secondary ridges occur between the lateral ridge and the edge of the endocarp. The endocarp wall which is 2-3 mm in thickness, con-

sists of tangentially oriented interweaving fibres. Evidence of radial fibres around lacunae is missing but as these fibres are not strongly lignified they are unlikely to be preserved in fossil material.

Wilkinsonia glencoensis (Rozefelds) comb. nov. (Fig. 4A-C).

1990a. *Athertonioides glencoensis* Rozefelds, pp. 123-4, fig. 3,A- C,D(left figure), E,H.

MATERIAL EXAMINED

Holotype, QMF17212 and additional specimens from the mid-Tertiary Glencoe locality (QML511), near Capella, CQ, figured by Rozefelds (1990a).

DIAGNOSIS

Endocarp variable in size, broad to suboval or rounded in outline, with prominent reticulate lacunose ornamentation, ridging poorly developed, length 36-43mm; width 25-34mm, height 14-21mm. A narrow lateral field with multiple irregular rows of depressions occurring between incipient ridge and edge of endocarp. Endocarp wall thick, but ligneous structure not preserved.

REMARKS

The two *Wilkinsonia* species differ in the width of the lateral field between the incipient ridge and edge of the endocarp. In *W. bilaminata* this zone is broad while in *W. glencoensis* and closely related modern genera of the Hicksbeachiinae, it is narrow. This broad field in *W. bilaminata* is reflected by the presence of multiple irregular rows of small depressions with accessory ridges between the incipient ridge and edge of the endocarp. *W. bilaminata* also appears to possess more pronounced longitudinal ridges than *W. glencoensis,* but these ridges along with the flattened appearance of the endocarp are in part, due to compression.

ENDOCARP MORPHOLOGY OF EXTANT GENERA IN THE HICKSBEACHIINAE

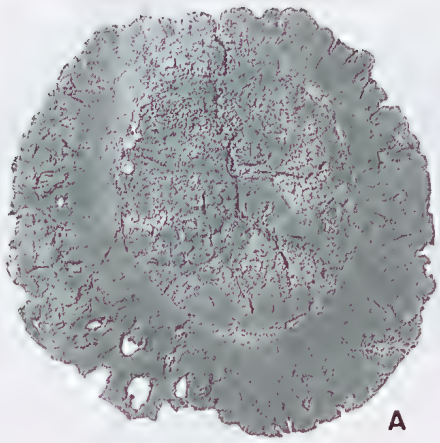
The endocarps of *Wilkinsonia* are strongly lignified which helped facilitate fossilization. The endocarp wall in *Heliciopsis* and *Athertonia* consists of tangentially and radially oriented fibres. In *Athertonia* the tangentially oriented fibre bands are numerous and diffuse while in *Heliciopsis artocarpoides*, the endocarp wall is thin and there are areas of lignified parenchyma interspersed around the tangentially oriented fibres (Fig. 4F, J). The radial fibres in *Athertonia* and *Heliciopsis* tend to be perpendicular to the outside edge of the endocarp. In *Heliciopsis* the radial fibres around the lacunae are variously oriented, and sometimes oblique to the endocarp wall (Fig. 4F-G,J-K).

In *H. artocarpoides* (Elm.) Sleumer the reticulate lacunose ornamentation is less developed and the ridging is less prominent than in *Athertonia* (Fig. 4H-I). Most species of *Heliciopsis* conform to the endocarp morphology in *H. artocarpoides* although material from Sumatra, figured as *Heliciopsis* sp. and tentatively compared with *H. incisa* by Sleumer (1955a:191,194) resembles *Athertonia* in having more thickly walled and more strongly ornamented endocarps. The endocarp wall of *Heliciopsis* sp. also lacks the internested lacunae typical of *H. artocarpoides* (Sleumer, 1955a).

Hicksbeachia is the only other genus of this subtribe in Australia with two allopatric species in eastern Australia (Weston, 1988). The endocarp of *Hicksbeachia pinnatifolia* lacks reticulate lacunose ornamentation. In the specimens of *Hicksbeachia* available there is not a clear separation between the inner ligneous (endocarp) and outer fleshy mesocarp. The endocarp in *Hicksbeachia*, in transverse section has prominent vascular bundles that are oriented longitudinally, (absent in *Heliciopsis* and *Athertonia*) and poorly lignified radial fibres extend from the outer edge of the endocarp into the fleshy mesocarp (Filla, 1926; Fig. 4L, M). Similarly in *Athertonia* and *Heliciopsis* radial fibres extend from the endocarp into the mesocarp, with persistent radial fibres evident around the lacunae. The endocarp (inner mesocarp of Weston, 1988) in *Hicksbeachia* consists of tangentially oriented fibres and lignified parenchyma.

The remaining genera in the Hicksbeachiinae; *Virotia* from New Caledonia lacks reticulate lacunose ornamentation of the endocarp while the fruit morphology of *Malagasia* from Madagascar is unknown (Johnson & Briggs, 1975; Virot, 1968).

FIG. 3. A-D, *Wilkinsonia bilaminata*. F. Muell. (NMVP53092). A,C, Internal view of endocarp wall × 1.2. B,D, External views of endocarp wall. Note prominent lacunae and the position of the incipient ridge indicated by arrows and wide lateral field × 1.3. E-F, *Athertonia diversifolia* (C.T. White) L. Johnson & B. Briggs × 1.5. E, Internal view and F, external view of endocarp wall.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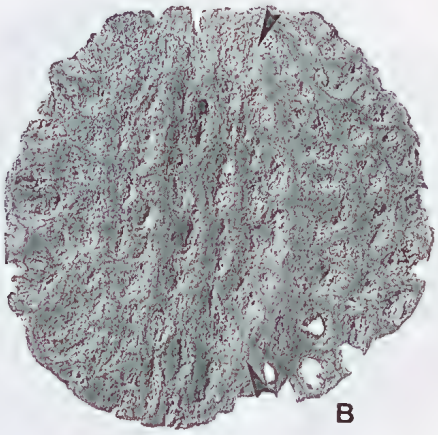
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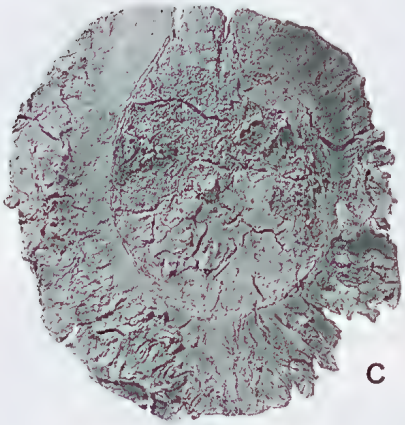
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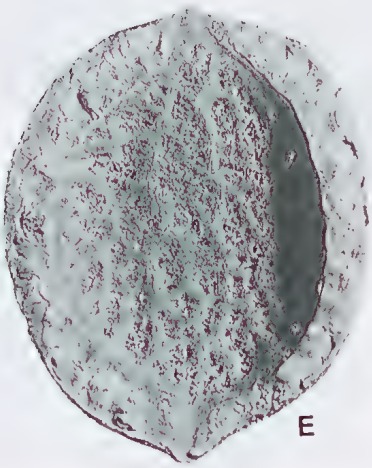
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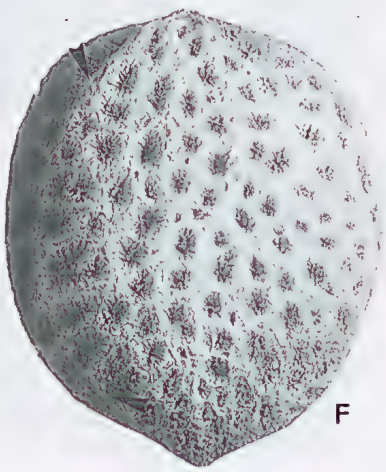
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CONCLUSION

The large endocarp, incipient ridge extending from the apex to the base and prominent reticulate ornamentation and arrangement of tangential fibres in *Wilkinsonia* strongly suggest affinities with genera in the subtribe Hicksbeachiinae (Sleumer, 1955 a,b; Rozefelds, 1990a). These external endocarp features are shared with *Athertonia* and *Heliciopsis* but are absent from *Hicksbeachia* and *Virotia.*

Wilkinsonia is more closely related to *Athertonia* than to *Heliciopsis.* In *Heliciopsis* the depressions on the endocarp wall tend to consist of internested small lacunae while in *Athertonia* and *Wilkinsonia* they tend to be separate and not internested. The endocarp wall in *W. bilaminata* is strongly ornamented, consists of separate lacunae surrounded by tangentially oriented fibres. The endocarp wall is relatively thin and the simple perpendicularly oriented lacunae in *Wilkinsonia* are similar to *Athertonia.* The internal ligneous structure of *W. glencoensis* is not preserved although the endocarps are thick and woody, have perpendicularly oriented lacunae as in *Athertonia* and differ from the relatively thin walled endocarps of *Heliciopsis* (Rozefelds, 1990a) (Fig. 4).

The fossil distribution of *Wilkinsonia* demonstrates that the subtribe Hicksbeachiinae was more widespread than at present (Fig. 1). *Wilkinsonia* is most closely related to *Athertonia* which is presently restricted to rainforest communities on the Atherton Tablelands of north eastern Queensland. Similarly the allopatric distribution of *Hicksbeachia,* and restriction to widely separated mesic rainforest communities is suggestive of a more widespread range for this genus during the Tertiary, which may have encompassed much of eastern Australia (Fig. 1). The close relationship of *Wilkinsonia* to *Athertonia,* and the presence of *Elaeocarpus* (Rozefelds 1990b) in this flora suggests that the Gulgong area during the mid-Miocene was dominated by rainforest. The taxonomic diversity and structure of these mid-Tertiary rainforests will be more fully understood when the affinities of the remaining fruits and seeds described by Mueller (1879, 1883) are recognized. This will only be achieved by the concurrent study and description of fruits and seeds of the contemporary Australian flora.

ACKNOWLEDGEMENTS

The Jabatan Perhutanan Herbarium, Sandakan, Sabah, Malaysia provided material of *Heliciopsis artocarpoides* (SAN 28114) for study. *Athertonia* and *Hicksbeachia* fruits were supplied by T. Irvine and P. Weston respectively. P. Jell and A. Drinnan gave helpful advice and comments on this paper. The Museum of Victoria provided funding for my visit, allowing access to collections and photographed the original plates from Mueller's papers. Most of the remaining photographs were taken by the photography section at the Queensland Museum. Information and/ or access to collections was provided by R. Jones (Australian Museum), E. Thompson (Museum of Victoria) and J. Pickett (Geological Survey of New South Wales).

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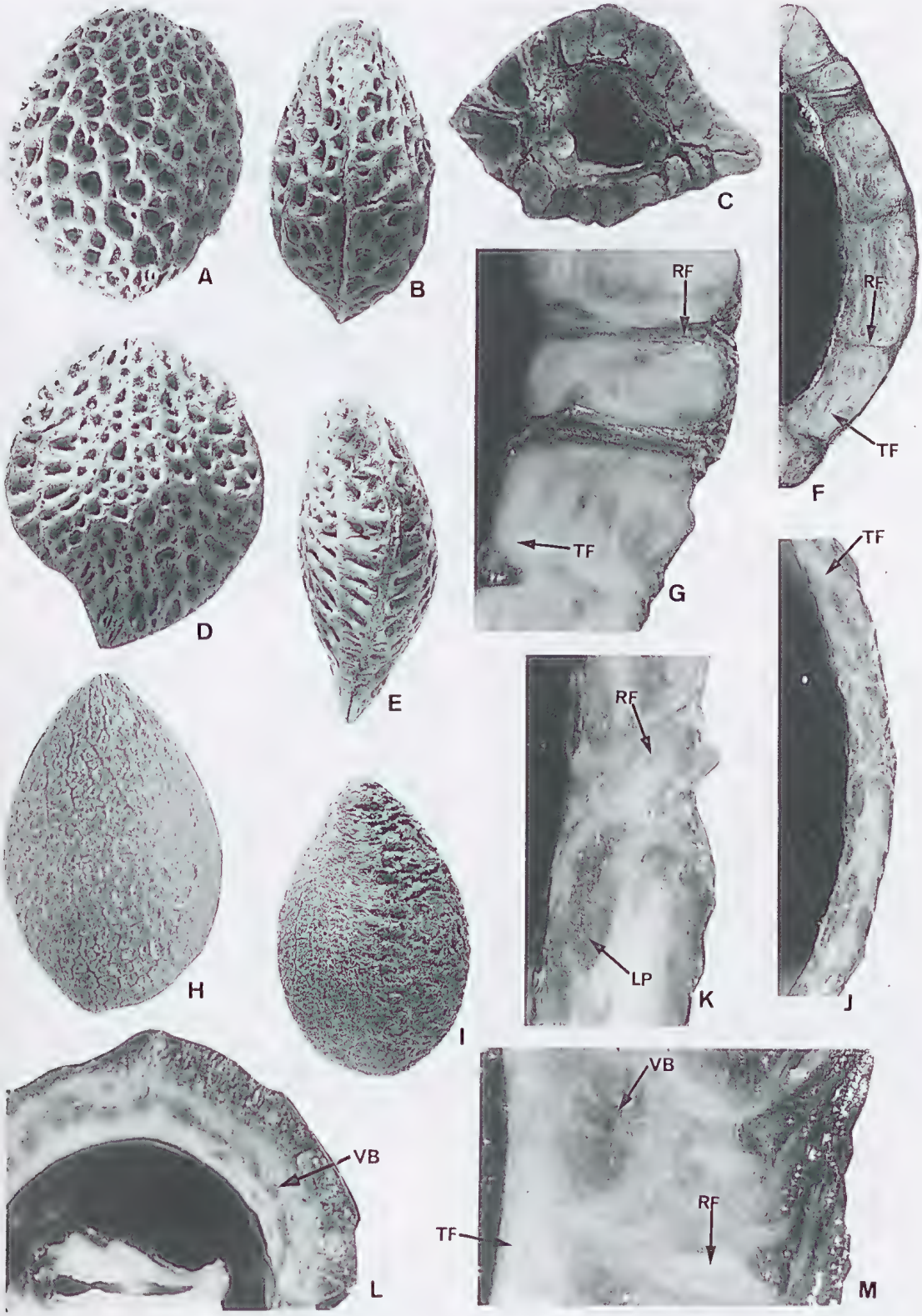
FIG. 4. A-C, *Wilkinsonia glencoensis* (Rozefelds). A, QMF17212, external view of endocarp note prominent simple lacunae × 1.2. B, lateral view of same specimen showing narrow lateral field between edge of endocarp and lateral ridge × 1.2. C, QMF17211, natural transverse section of exoocarp × 1.7. D-G, *Athertonia diversifolia.* D. External views of endocarp × 1.1. E, Lateral view of same specimen showing narrow lateral field × 1.1. F- G, Transverse section of endocarp wall showing strongly lignified tangentially oriented fibres (TF) and poorly lignified radially oriented fibres (RF) F × 2.3, G × 6.7. H- K, *Heliciopsis artocarpoides* (SAN 28114). H, External view of endocarp showing internested lacunae × 1.7. I, lateral view of same specimen showing internested lacunae of the endocarp wall and fine radial fibres that extend into mesocarp, the thin exocarp wall has flaked away from the mesocarp, × 1.5. J-K, transverse section of endocarp wall showing radial fibres (RF), transverse fibres (TF) and ligneous parenchyma (LP), J × 5.8, K × 20.5. L-M, Transverse sections of *Hicksbeachia pinnatifolia* F. Muell., endocarps showing vascular bundles (VC), radial fibres extending from near the mid-region of the endocarp extending into the mesocarp; tangential fibres occur along inner wall of endocarp, L × 4.3, M × 17.0.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TERTIARY OCCURRENCE OF THE FERN *LYGODIUM* (SCHIZAEACEAE) IN AUSTRALIA AND NEW ZEALAND

A.C. ROZEFELDS, D.C. CHRISTOPHEL AND N.F. ALLEY

Rozefelds, A.C., Christophel, D.C. & Alley, N.F. 1992 06 29: Tertiary occurrence of the fern *Lygodium* (Schizaeaceae) in Australia and New Zealand. *Memoirs of the Queensland Museum* 32(1): 203-222. Brisbane. ISSN 0079-8835.

Lygodium is ubiquitous in early Tertiary floras of Australia. Sterile and fertile leaves of the climbing fern *Lygodium* are found in Eocene deposits from Anglesea (Victoria), Maslin Bay and Golden Grove (South Australia) and in the early Tertiary from Dinmore in Queensland (*L. dinmorphyllum* Churchill, 1969). Sterile material is known from Late Eocene/Early Oligocene sediments at Cethana (Tasmania) and the Middle Eocene at Temuka, in New Zealand.

New material from the Golden Grove, Maslin Bay and Anglesea localities including sterile and fertile pinnules, spores, and cuticular structure is referred to *L. dinmorphyllum*. The fertile pinnae contain spores of *Cyathidites splendens* Harris, 1965. This palynomorph has a Late Cretaceous (Maastrichtian) to Pliocene range in southern Australia. The Australian species is very similar to the Eocene Chilean *L. skottsbergii* Halle, 1940, in sterile and fertile pinnule morphology. Heterophylly presents problems in interpreting variation in fossil *Lygodium*.

☐*Lygodium, Schizaeaceae, Cyathidites splendens, Tertiary, palynology, palaeobotany, biogeography, Australia, New Zealand.*

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Extant *Lygodium* is a pantropical climbing fern with temperate outliers occurring in New Zealand (*L. articulatum* A. Rich.), eastern United States (*L. palmatum* (Bernh.) Swartz and Japan [*L. japonicum* (Thunb.) Sw.]. About 40 species are known world wide with four occurring in Australia (Holttum, 1959). The Australian species *L. japonicum* (Thunb.) Sw., *L. flexuosum* (L.) Sw., *L. microphyllum* (Cav.) R. Br. and *L. reticulatum* Schkuhr are tropical occurring in northern and eastern Australia. In this paper, fossil *Lygodium* leaves including sterile and fertile pinnules are described from Dinmore (Queensland), Maslin Bay and Golden Grove (South Australia) and Anglesea (Victoria) and a number of other localities in southern Australia and New Zealand (Fig. 1). Previous records of *Lygodium* or *Lygodium*-like ferns are reviewed. Problems inherent in classifying and describing variable taxa are discussed.

PREVIOUS RECORDS OF FOSSIL *LYGODIUM* IN AUSTRALIA AND NEW ZEALAND

Lygodium or *Lygodium*-like fossils have been reported by Johnston (1894), Ettingshausen (1886, 1888), Shirley (1898), Churchill (1969), Hill et al. (1970), Douglas (1978), Peters & Christophel (1978) and Christophel & Greenwood (1987). Churchill's material was the first unequivocal fossil evidence of the genus in Australia. The taxa described in the 19th century were based on fragmentary sterile pinnules but none can be confidently assigned to *Lygodium* (Churchill, 1969). Of these taxa the type of *Osmunda tasmanica* Johnston from Glenora, could not be located in collections in Tasmania (R. S. Hill & N. Kemp, pers. comm.). The holotype of *L. strzeleckii* Ettingshausen, 1886, collected from the Vegetable Creek locality was restudied and prepared further (Fig. 3A) but referral to *Lygodium* is dubious because it is based upon small pinnule fragments with abraded margins. The Late Triassic *Lygodium antiquorum* Shirley, 1898 from the Ipswich Coal Measures is based upon a trilobate seed fern or fern pinnule (Fig. 3F) with no evidence of sporangia, and is not referable to *Lygodium* as Walkom (1917) indicated.

Churchill (1969) described *L. dinmorphyllum* based upon two fertile pinnules from the early Tertiary Redbank Plains Formation at Dinmore in south eastern Queensland. Hill et al. (1970) recorded sterile *Lygodium* pinnules from Dinmore, which they referred to *L. skottsbergii*. Douglas (1978) figured a fertile *Lygodium* pinna

from Anglesea in Victoria. A fern frond tentatively compared with *Lygodium* has also been figured from the Cenomanian Winton flora of Western Queensland (Peters & Christophel, 1978). Christophel & Greenwood (1987) recorded *Lygodium* from the Golden Grove locality.

Additional material was collected from Dinmore and Anglesea by ACR and DCC respectively over a number of years. *Lygodium* has also been recently collected from the Middle Eocene Maslin Bay and Golden Grove floras (South Australia) and the Late Eocene/Early Oligocene Cethana flora of Tasmania (R. Carpenter, pers. comm.). *Lygodium* pinnae have also been recognized from Temuka in New Zealand (D. Mildenhall, pers. comm. 1986).

LOCATION OF SITES AND AGES OF FLORAS

The Dinmore site in the Redbank Plains Formation, south eastern Queensland is of Paleocene/Eocene age (Day et al., 1983). This largely undocumented flora includes ferns, Podocarpaceae and dicotyledonous leaves (Hill et al., 1970; Selling, 1950).

The diverse Anglesea flora occurs in the Middle Eocene Eastern View Coal Measures, and while *Lygodium* occurs in most lenses the majority come from the *Gymnostoma* lens (Christophel et al., 1987). Elements of the Maslin Bay flora were described by Blackburn (1981) from a carbonaceous clay lens in the Middle Eocene North Maslin Sands (McGowran et al., 1970; Alley, 1987). A well preserved flora from the North Maslin Sands at Golden Grove, north of Adelaide is also Middle Eocene in age. A recent overview of the flora has been provided by Christophel & Greenwood (1987).

The Late Eocene/Early Oligocene Cethana flora has yielded *Nothofagus* leaves (Hill, 1984), and the remaining flora, which includes 'tropical'

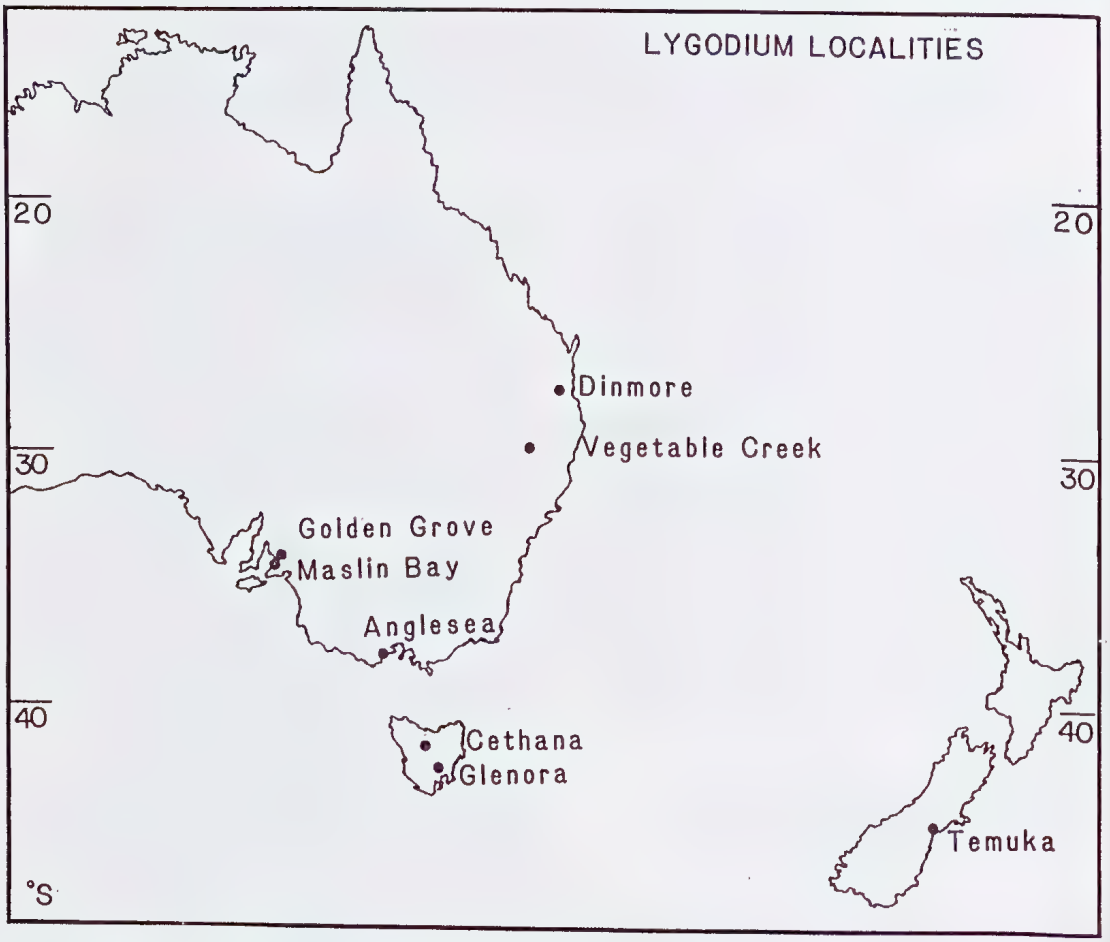
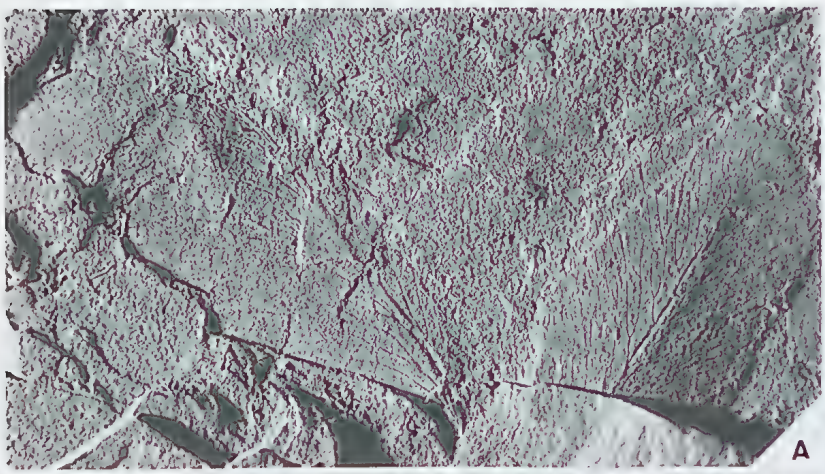


FIG. 1. Fossil *Lygodium* localities in Australia and New Zealand.

FIG. 2. *Lygodium articulatum* A. Rich. from Fairy Falls Track, Waitakere Range, South of Auckland, New Zealand. DSIR, Christchurch CHR153015. Note abscission nodes at base of sterile pinnules and the varying development of lamina between sorophores. [Photograph supplied by Bryony MacMillan, DSIR, Christchurch, New Zealand].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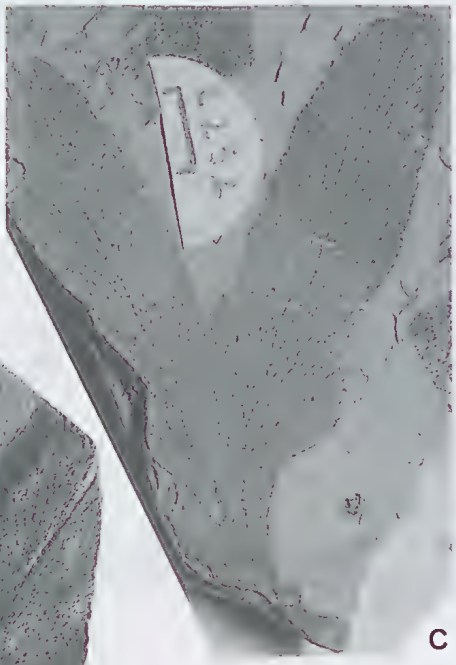
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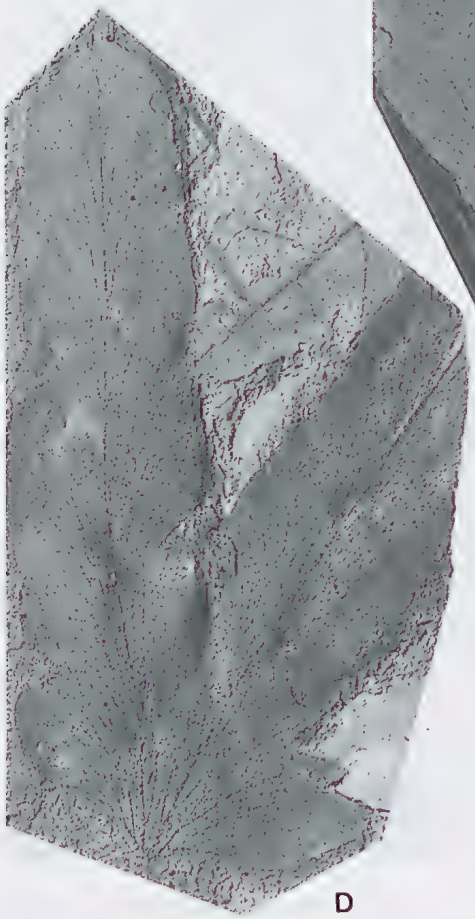
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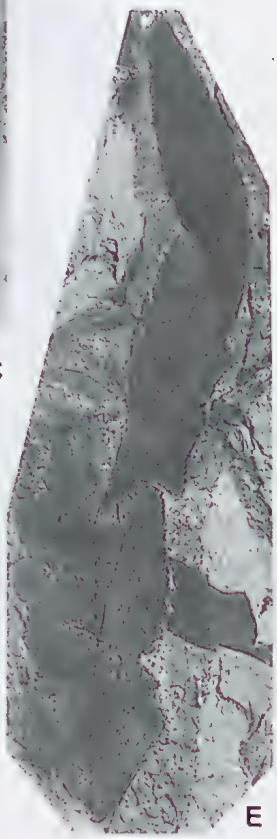
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rainforest elements is presently being studied (R. Carpenter, pers. comm., 1987). The geology and stratigraphic information on the Temuka potteries clay pits in New Zealand indicates an Eocene age for this flora (Wellman, 1953; Gair, 1967). Specimens from these two localities were not available for study.

METHODS AND PRESERVATION OF FOSSILS

The Dinmore, Cethana and Vegetable Creek materials are preserved as impressions in fine grained mudstones lacking cuticle. Latex peels of the surface of sterile *Lygodium* pinnules from Dinmore, examined with a SEM, yielded no cellular information (D. Dilcher, pers. comm.). However, SEM examination of fragments of the original specimen do show some cellular information (Fig. 11A,B). The Maslin Bay and Anglesea specimens are preserved as compressions or impressions while *Lygodium* leaves and sorophores from Golden Grove are 'mummified'. The method for preparing 'mummified' leaves follows that of Christophel (1984). The Golden Grove *Lygodium* leaves are usually opaque and could not be studied using the fluorescence technique of Friedrich & Schaarschmidt (1977). Small areas of venation in these specimens were illuminated using narrow beams of light from cold light sources.

The mummified sorophores and small fragments of leaf cuticle from Golden Grove were cleaned with concentrated HF acid for a few days and the sporangia were gently macerated to release spores. Spores were studied and photographed with a Zeiss Photomicroscope 111. Fragments of cuticle from the sorophores and leaves were washed in distilled water, airdried and sputter coated with platinum. Material was examined with a JEOL JSM 840 scanning electron microscope with lanthanum hexaboride filament at 5kv.

Lygodium examined in this paper (Appendix A) includes material from the Queensland Museum (QMF), Geological Survey of Queensland (GSQF), University of Queensland (UQF), Museum of Victoria (NMVP), University of Tasmania (UTC), University of Adelaide (Maslin Bay, UAS; Golden Grove, UAG), and Geological Survey of New Zealand (GSNZ). Modern *Lygodium* material collected by ACR for this study, will be donated to the Queensland Herbarium (BRI).

SYSTEMATIC PALAEOBOTANY

Family SCHIZAEACEAE

Lygodium Sw.

The new *Lygodium* material from the various Australian localities is considered to be conspecific with *L. dinmorphyllum* Churchill from Dinmore in south eastern Queensland. An emended diagnosis of this taxon including information on spores, cuticle and foliar heteromorphism is given, as Churchill's description only covered the gross morphology of the fertile pinnules.

Lygodium dinmorphyllum Churchill, 1969
(Figs 4-10)

1969 *Lygodium dinmorphyllum* Churchill, pp. 257-265, fig.2.
1970 *Lygodium skottsbergii* Halle, Hill et al., pl. Czll, fig. 1.

EMENDED DIAGNOSIS

Sterile pinnules asymmetrical, usually 2-3 lobed, although unilobate, quadrilobate and pentalobate pinnules occur. Lateral lobes tend to be longer than central lobes. Pinnule base is cuneate to truncate, apex rounded to acute. Pinnules petiolate, lacking abscission node at pinnule base. Venation palmate, dichotomously branching from the central vein, on each lobe, two to three times before reaching leaf margin. Leaf length variable, maximum lobe length about 110mm. Pinnule margin variable, undulose in larger specimens, smooth in small pinnae, rarely lobed. Pinnules probably hypostomatic. Anticlinal walls of abaxial epidermis strongly sinuous, stomata anomocytic. Stomatal apparatus 30μm long, (29-32μm) and 27μm wide (25-32μm).

Fertile pinnules in branched axes often lack lamina, although lamina sometimes present as narrow wing or flange at the base of sorophores. Individual sorophores variable in size, ranging

FIG. 3. A, Holotype, *Lygodium strzeleckii* Ettingshausen, from Vegetable Ck, GNSWF8820, × 3. B,C, Cethana ferns. B, fern aff. *Lygodium*, sterile pinnule UTC235. C, Bilobate sterile *Lygodium* pinnule UTC232, × 2. D,E, Temuka *Lygodium*, New Zealand. D, GSNZ25/90, × 1.7. E, GSNZ25/92, × 2. F, Holotype, *Lygodium antiquorum* Shirley, GSQF143, × 3.5. [D. Mildenhall (DSIR, New Zealand Geological Survey, Lower Hutt) and R. Carpenter (University of Tasmania) supplied photographs of the Temuka and Cethana specimens respectively].

from about 4.0-14.0mm in length, often united in groups of 2-4. Spores referable to *Cyathidites splendens* Harris, 1965. Sinuosity of anticlinal walls of epidermis on sorophore lamina not as pronounced as in sterile pinnules.

REMARKS

The Golden Grove and Anglesea localities have yielded *Lygodium* sorophores containing *C. splendens* spores. *C. splendens* is also a common palynomorph in the Maslin Bay palynoflora. While spores have not been isolated from the Dinmore sorophores and the cuticle is poorly known, it seems preferable to refer the new material to *L. dinmorphyllum* than erect a doubtfully distinct taxon. Based upon the widespread distribution of *C. splendens* in the early Tertiary and Late Cretaceous in Australia it seems likely that the Dinmore sorophores also had *C. splendens* spores. *Lygodium dinmorphyllum* is closely comparable with *L. skottsbergii* but is considered distinct based upon spores and cuticular information. Halle (1940: 259) noted that the spores of *L. skottsbergii* are finely punctate or almost smooth and hence differ from *C. splendens*.

The only contra-indication that the *Lygodium* material from Australia may include a number of taxa is the variation in the angle of lower order branching in the fertile axes at different localities. In a relatively complete non-distorted specimen from Anglesea (Fig. 8D), the angle of branching is (130-150°), which is similar to that of modern *L. articulatum* (Fig. 2). The Dinmore material typically has acutely angled lower order branching in the fertile pinnae, i.e. (75-85°) (Fig. 4A, G,H). Relatively complete and undistorted fertile axes have not been collected from Golden Grove or Maslin Bay so the angle of branching in the fertile axes from these localities is unknown. The systematic implications are difficult to assess because insufficient material has been collected from enough localities to assess variation.

FOLIAR HETEROMORPHISM IN EXTANT *LYGODIUM*

Foliar heteromorphism is the production of morphologically variable leaf types on the same individual (Eckenwalder, 1980). Changes in the size and shape of successive leaves can be due to heteroblastic development (Wareing & Phillips, 1982). This may occur in the transition from juvenile to adult leaves or may result from environmental factors. In *Lygodium*, transition from sterile to fertile pinnae results in morphologically distinct pinnae. Pinnae intermediate in character between sterile and fertile pinnules occur in *L. articulatum* and *L. palmatum*. The lamina in the fertile pinnae of the extant species *L. articulatum* and *L. palmatum* is very reduced and the pinnules are strongly dimorphic (Fig. 2; Manchester & Zavada, 1987, figs 9,11). The degree of lamina reduction varies in fertile leaflets of *L. articulatum* (Fig. 2).

In *Lygodium*, there is great plasticity of form in sterile and fertile pinnae, and fusion of pinnules occurs. Sterile leaflets in extant *L. articulatum* are characteristically unilobate although fused bilobate pinnules also occur. Fusion of pinnules may explain some variation in fossil material from Australia.

Aberrant pinnules with accessory lobing were collected from Dinmore, Maslin Bay and Golden Grove (Fig. 9G,H) and were also figured for *L. kaulfussi* Heer, 1861 by Manchester & Zavada (1987). In modern *L. reticulatum* from north eastern Queensland similarly deformed leaves also occur.

FOSSIL *LYGODIUM* MORPHOLOGY

Taxonomic treatments of extant *Lygodium* are based upon the form of sterile and fertile pinnules, spores, venation and mode of branching. Holttum (1959: 39) commented that 'there is so much variation in leaflet form due to the age of the plant,

FIG. 4. Fertile *Lygodium dinmorphyllum* pinnules from Dinmore. A, QMF14465, × 1.9, sporangial head free of lamina. B, QMF14530, x 2, lamina around sporangial heads. C,D, GSQF12973. C, ×2.8. D, ×1.0. E,F, QMF14361. E, ×3.1. F, × 1. G,H, QMF12544. G, × 3.3. H, × 1.

FIG. 5. Sterile *Lygodium dinmorphyllum* pinnules from Dinmore, illustrating variation in pinnules. A, QMF18035. B, QMF15320. C, QMF14365. D, QMF2858. E, QMF15319. F, QMF14974. G, QMF14363. H, UQF32006. I, GSQF12974. J, QMF14366. All natural size.

FIG. 6. Sterile *Lygodium dinmorphyllum* pinnules from Dinmore, illustrating variation. A, QMF 18035, × 1. B, QMF14809, × 2. C, UQF32006, × 1.4. D, QMFl4363, × 3.5.

FIG. 7. Fertile and sterile *Lygodium dinmorphyllum* pinnules from Maslin Bay. A,B, Sterile trilobate pinnule, UAS715. A, × 2. B, × 1. C, Fertile pinnuleUAS3524, × 5. D,E, Sterile unilobate pinnule with poorly developed secondary lobe, UAS2274. D, × 2.3. E, × 1.0. F,G, Bilobate sterile pinnule, UAS1211. F, × 1.9. G, × 1.0.

Figure 4

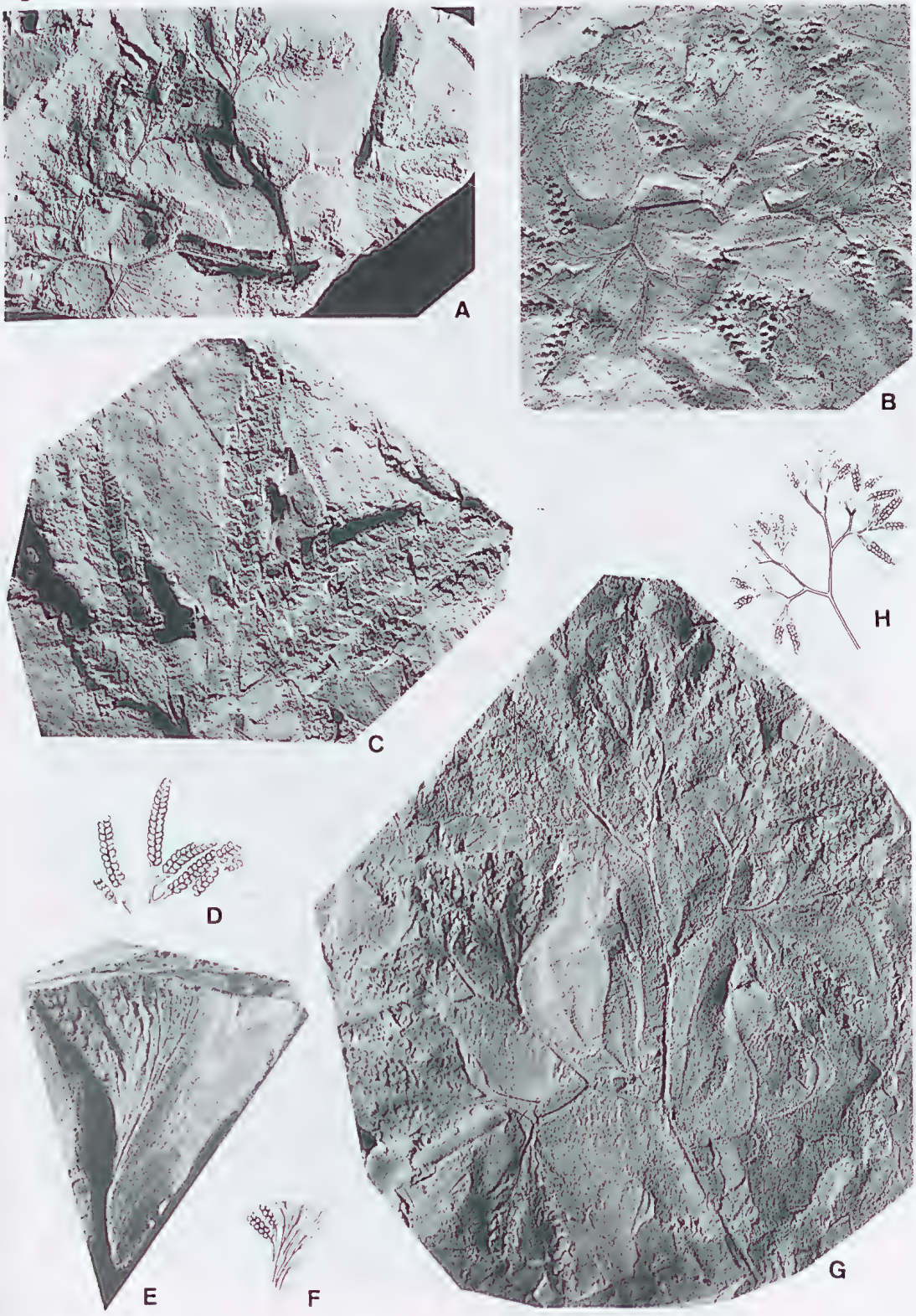


Figure 5

Figure 6

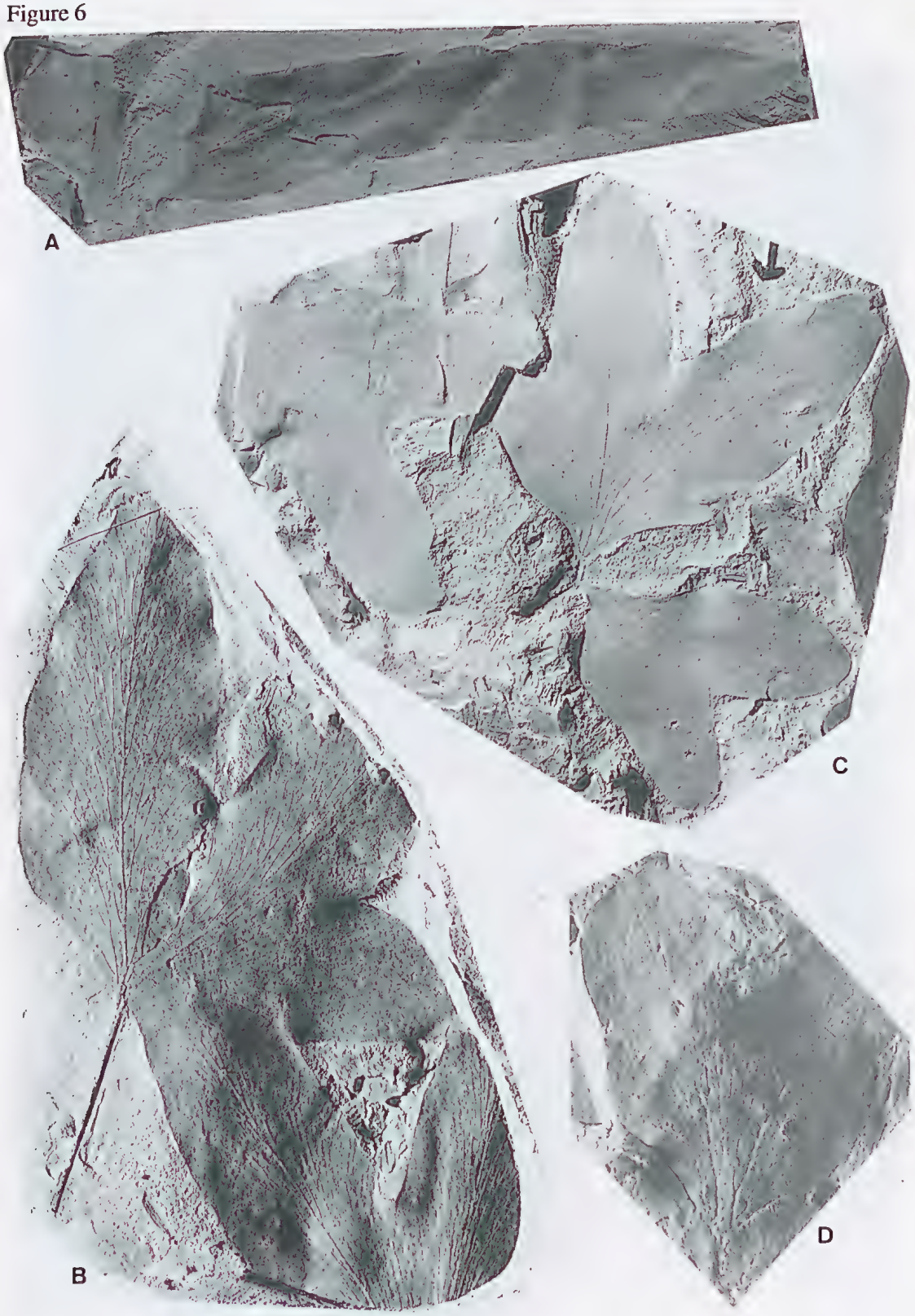


Figure 7

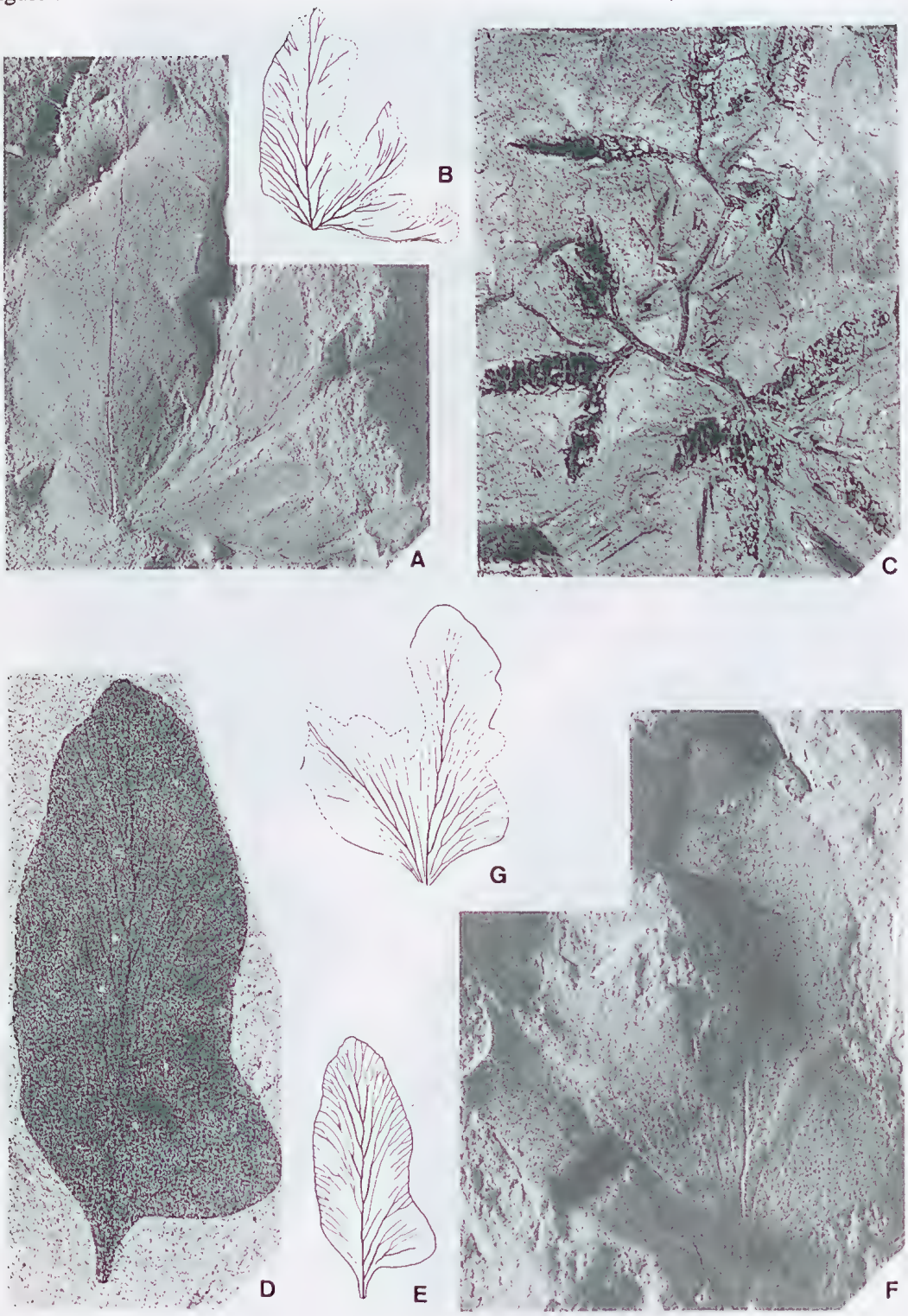


Figure 8

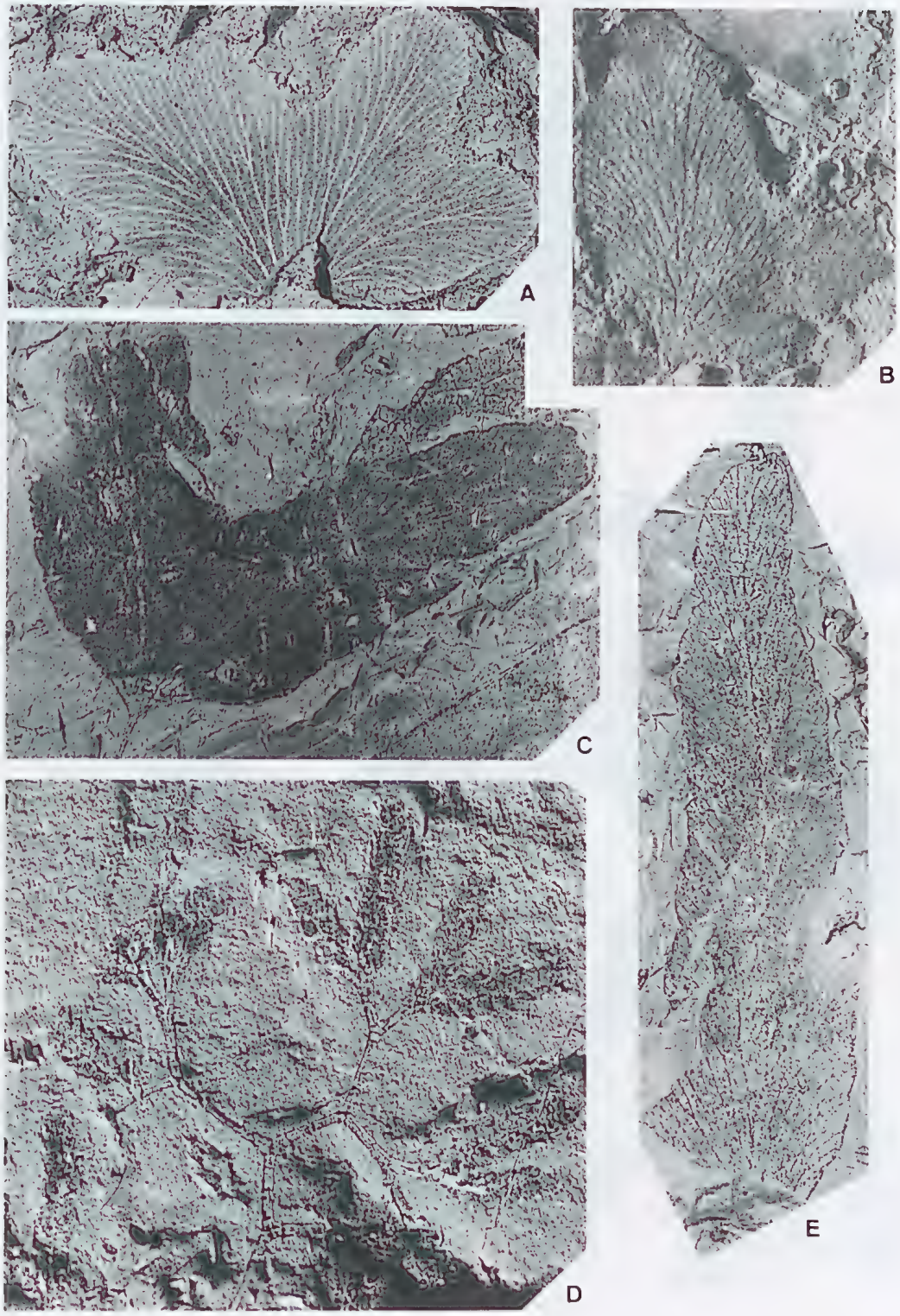


Figure 9

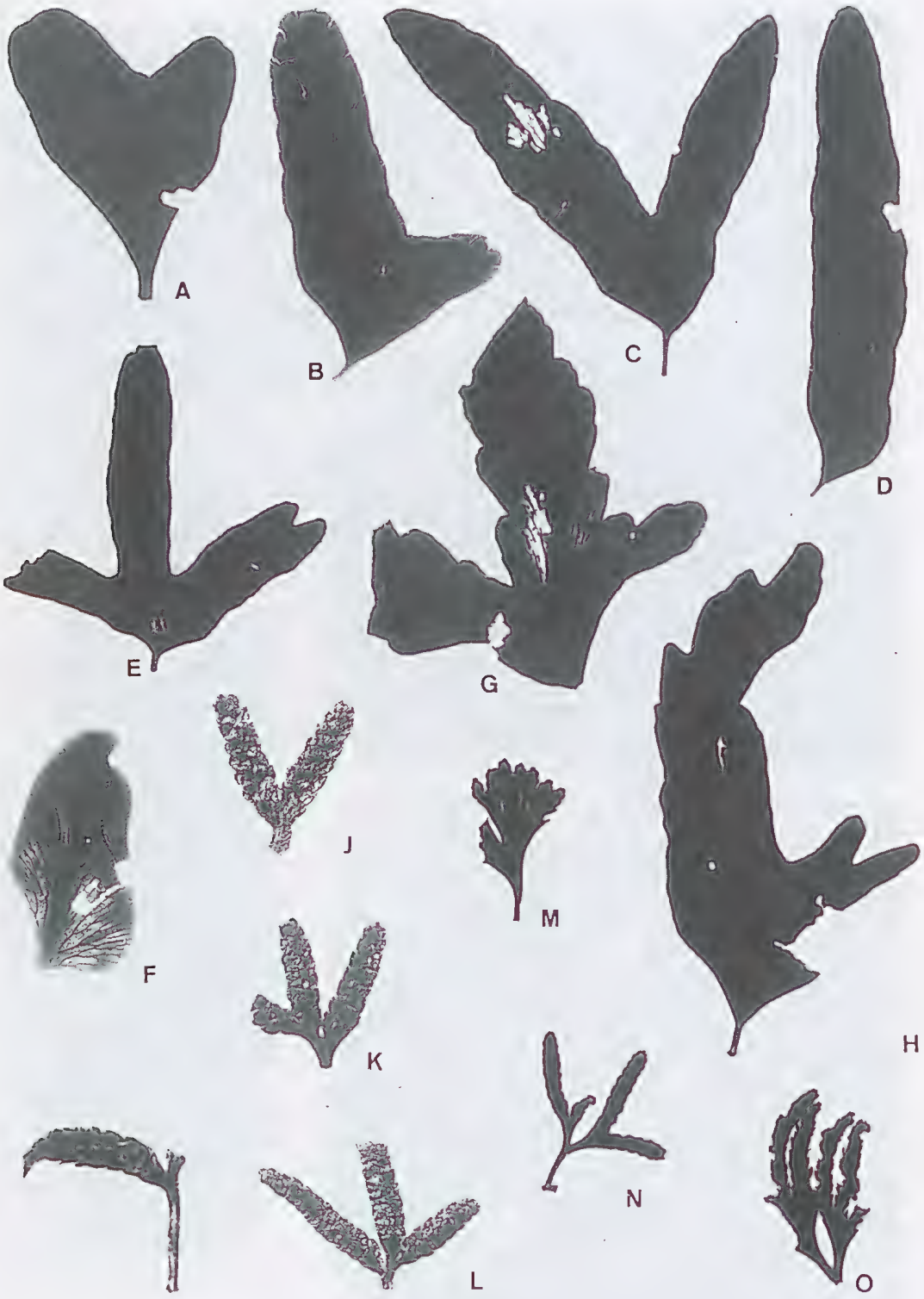


Figure 10

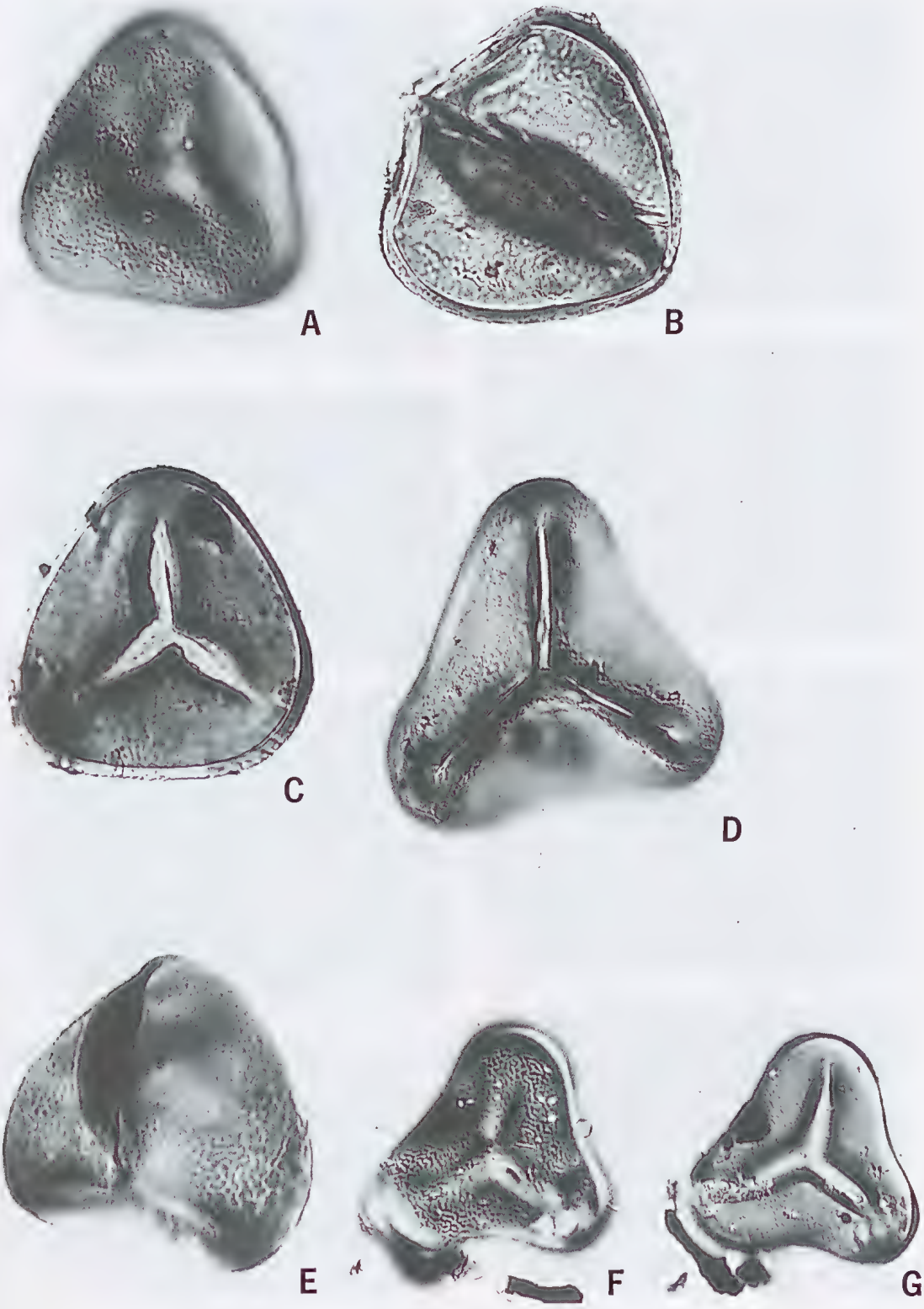
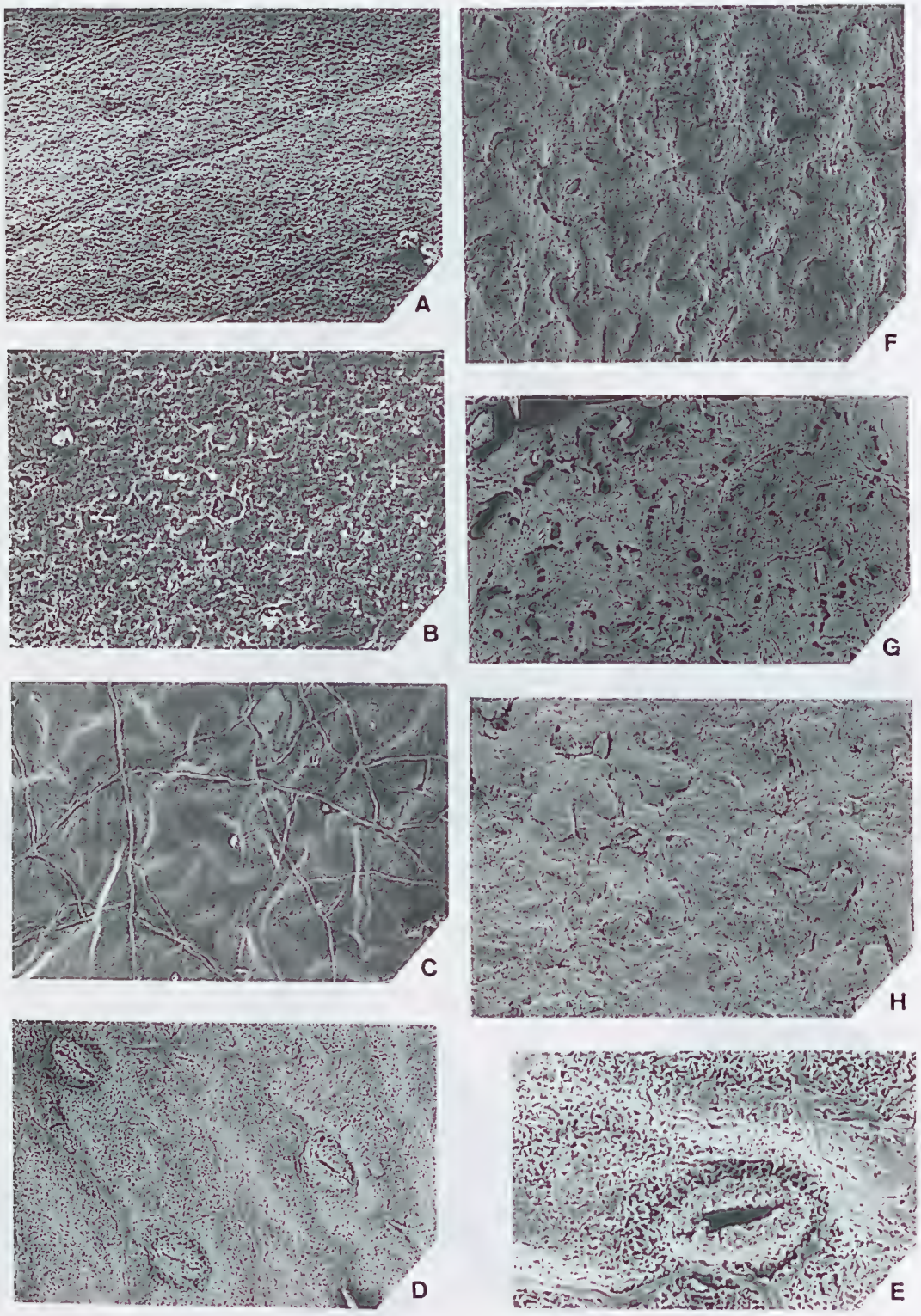


Figure 11



height above ground and perhaps polyploidy and hybridization that even with ample material it is not easy to give specific limits'. Fossil *Lygodium* presents further problems due to the incomplete and fragmentary material available for study. The overlap in morphology and variation in sterile *Lygodium* pinnules from sites in Australia and New Zealand is presented in Table 1. As Dinmore and Golden Grove have yielded the largest amount of vegetative and fertile material, discussion centres on material from these two localities. The strongly dimorphic sterile and fertile pinnules occur in association at Dinmore, Golden Grove, Anglesea and Maslin Bay. Material from Dinmore indicates that the sterile and fertile *Lygodium* pinnules can be referred to the same plant (Fig. 4E-F).

Sterile Pinnule Morphology

Fossil *Lygodium* pinnules from the various sites are asymmetrical and palmately lobed. The number of lobes in sterile *Lygodium* was used by Berry (1930) to define new fossil taxa, although it is an extremely variable feature. *Lygodium* pinnules at most sites, but particularly at Dinmore and Golden Grove, exhibit considerable variation in the number and degree of lobation (Table 1). At Dinmore, unilobate and trilobate and bilobate and trilobate pinnules have been found in organic connection (Figs 5E,H,6C). In the extant New Zealand species *L. articulatum*, unilobate pinnules predominate but fused bilobate pinnules occur. Similarly, in fossil *Lygodium* from Dinmore, bilobate and trilobate pinnules are the most common, although rare quadrilobate and pentalobate pinnules occur (Fig. 5B,I). These are interpreted as resulting from the fusion of trilobate with unilobate and bilobate pinnules. Bilobate and trilobate pinnules also predominate in the Golden Grove, and Maslin Bay localities (Table 1). The Australian fossil *Lygodium* pinnules resemble extant *L. palmatum* in having multilobate pinnules but like *L. kaulfussi* Heer, they differ in their larger, more elongate pinnules.

All the major localities in Australia have yielded sterile pinnules with petiolules. In most specimens the petiolules are short (<3.0mm long), except a few specimens from Dinmore which have a preserved petiolule length of up to 15.0 mm (Fig.

FIG. 8. Sterile and fertile *Lygodium dinmorphyllum* from Anglesea. A, Quadrilobate sterile pinnule, NMVP178150, × 2.3. B, Bilobate sterile pinnule, NMVP178148, × 2. C, Bilobate sterile pinnule, NMVP178149, × 2.2. D, Sorophore, arrow indicates prominent obtuse branching of sorophore, NMVP165681, × 4.6, E, Fragmentary single lobe of large sterile pinnule, NMVP178145, × 2. [Photographs of NMVP165681 provided by J. Douglas].

FIG. 9. Sterile and fertile *Lygodium dinmorphyllum* from Golden Grove. A-H, Sterile pinnules. A, Small pinnule, UAG3024, × 2.5. B, Bilobate pinnule, UAG3022, × 1.5. C, Bilobate pinnule, UAG2604, × 1.6. D, Unilobate pinnule, UAG3004, × 1.2. E, Trilobate pinnule, UAG1379, × 1.2. F, Small unilobate pinnule, UAG3003. × 1. G, Aberrant trilobate pinnule with multiple accessory lobing, UAG2718, × 1.7. H, Aberrant bilobate pinnule with multiple accessory lobes, UAG3018, × 1.5. I-O, Terminal sorophores, all × 4. I, UAG3037. J, UAG3036. K, UAG3039. L, UAG3038. M, UAG3042, × 1.7. N, UAG3040, × 1.7. O, UAG3041, × 1.5.

FIG. 10. Spores macerated from *Lygodium dinmorphyllum* sporophores from Golden Grove and Anglesea; and late Paleocene *Cyathidites splendens* from the Lake Eyre Basin. A, Ornamentation of distal surface of *L. dinmorphyllum* spore, Golden Grove. Original magnification × 40. Zeiss location 20.8/87.4; England Finder Location V 17/0. B, Equatorial view of *L. dinmorphyllum* spore, Golden Grove, showing thickened exine and reduced ornamentation. Original magnification x 40. Zeiss location 19.6/99.0; England Finder Location U 29/0. C, Proximal view of *L. dinmorphyllum* spore, Golden Grove, showing slightly thickened radials and gaping laesura. Original magnification × 40. Zeiss location 19.6/122.5; England Finder Location U 53/0. D, Proximal view of *L. dinmorphyllum* spore, Golden Grove, showing thickened labra and reduced ornamentation. Original magnification × 40. Zeiss location 14.8/101.3; England Finder Location P 31/0. E, Oblique equatorial view of *L. dinmorphyllum* spore, Anglesea, PB5304, with strongly developed rugulate ornamentation. Original magnification, × 40. Zeiss location 18.8/104.9; England Finder Location T 35/0. F, Distal surface of *C. splendens*. Muloorina 2 well, 34 metres depth, showing rugulate and verrucate ornamentation. Original magnification × 16. Zeiss location 10.5/95.8; England Finder Location L 26/1. G, Proximal surface of same specimen with reduced ornamentation, gaping laesura and slightly thickened radials.

FIG. 11. SEM of fossil and modern *Lygodium* cuticle. A,B, Anticlinal walls of epidermis in sterile *L. dinmorphyllum* pinnules from Dinmore, QMFI8904. A, Venation and general appearance of leaf impression, note venation × 50. B, Sinuous anticlinal walls of epidermis × 140. C, SEM of adaxial surface of *L. articulatum* cuticle, showing ?wax covered cuticle and fungal hyphae, × 270. D,E, SEM of abaxial surface of *L. articulatum* cuticle. D, showing arrangement of stomata × 260, E. Detail of stomata × 700; F-H, Cuticle from *L. dinmorphyllum* leaves and sorophores from Golden Grove. F, Abaxial surface, showing arrangement of stomata, UAG3021, × 320. G, Cuticle from fertile sorophore of UAG3041, × 430. H, ?Adaxial surface of leaf cuticle, UAG3021, × 350. [Photographs of Figs 11A,B supplied by M.E. Dettmann and H.T. Clifford].

TABLE 1. Comparison of the morphology of sterile *Lygodium* pinnules from localities in Australia and New Zealand.

LOCALITY	PINNULE SHAPE	VENATION	PINNULE APEX	PINNULE BASE	REFERENCES
L. dinmorphyllum					
Dinmore, Queensland	asymmetrical/palmate; bi., tri., quad., pentalobate	dichotomous	acute, obtuse, retuse	cuneate, truncate	Churchill, 1969; Hill et al., 1970
Anglesea, Victoria	asymmetrical/palmate; bilobate, quadrilobate	dichotomous	acute, obtuse, retuse	cuneate	Douglas, 1978
Maslin Bay, S. Aust	asymmetrical/palmate; uni., bi., trilobate	dichotomous	acute, obtuse	cuneate, truncate	—
Golden Grove, S. Aust	asymmetrical/palmate; uni.,bi., trilobate	dichotomous	acute, obtuse, retuse	cuneate, truncate	Christophel and Greenwood, 1987
Lygodium sp.					
Cethana, Tasmania	asymmetrical/palmate?; uni., bilobate	dichotomous	acute?, obtuse	cuneate	—
Temuka, New Zealand	asymmetrical/palmate?; uni., trilobate	dichotomous	obtuse, acute	truncate	
Vegetable Creek, N.S.W (*L.strzeleckii*)	unilobate	dichotomous	obtuse	—	Ettingshausen, 1886
L. skottsbergii					
Chile (fossil)	asymmetrical/palmate; bi., trilobate	dichotomous	acute, obtuse	truncate, broady cuneate	Halle, 1940
L. articulatum					
New Zealand (extant)	usually unilobate, rarely bilobate	dichotomous	acute	cuneate	

6B). The end of the petiolule in the Golden Grove material is frequently enlarged indicating a point of attachment and probably also dehisence (Fig. 9B-E,H). In extant *L. articulatum*, sterile and fertile pinnules lack a petiolule, and the abscission node occurs at the leaf base (Fig. 2). This feature also occurs in the fossil *L. kaulfussi* and was used by Manchester and Zavada (1987) to differentiate between *L. kaulfussi* and *L. skottsbergii*. *Lygodium skottsbergii* and the fossil Australian material resemble extant *L. palmatum* in that their leaflets are firmly affixed to short petiolules (Manchester & Zavada, 1987).

The pinnule margins in *L. dinmorphyllum* are entire to undulose with some specimens showing irregular lobation (Fig. 9G,H). One of the Cethana specimens (Fig. 3B) is irregularly serrate and is tentatively referred to *Lygodium*. The serration is accentuated by tearing of the leaf lamina and margins during fossilization. The other specimen is asymmetrical and bilobate (Fig. 3C) and comparable to other *Lygodium* material. The concavely curved basal margin of the pinnule is similar in both specimens. This feature occurs consistently in most of the Tertiary *Lygodium* material in Australia. The base of the pinnule is typically cuneate or truncate while in *L. kaulfussi* it is rounded to obtuse or cordate (Manchester & Zavada, 1987).

The venation in the fossil Australian and New Zealand material is dichotomous, branching 2-3 times before reaching the margin. The venation of the Australian *Lygodium* material appears indistinguishable from *L. kaulfussi* from the Eocene material from Wyoming figured by Manchester & Zavada (1987). Dichotomous venation is typical of most *Lygodium* species except those with reticulate venation, e.g. *L. reticulatum*.

Preservation of the mode of branching and evidence of the climbing habit which is characteristic of modern species in this genus is rare in the fossil record and is unlikely to occur in those species whose pinnules dehisce at senescence. The only evidence of the mode of branching in fossil *Lygodium* comes from impressions at Dinmore.

Fertile Pinnule Morphology

The sorophores of *L. dinmorphyllum*, like those

of *L. kaulfussi* and the extant species *L. palmatum* and *L. articulatum*, are produced terminally on branched axes. The sorophores vary in size, reflecting their position on the plant and stage of development. *Lygodium skottsbergii*, *L. articulatum* and *L. dinmorphyllum* all show variation in reduction of lamina in fertile pinnae. The fertile pinnae of *L. articulatum* vary in the free lamina between sorophores (Fig. 2) and *L. skottsbergii* shows similar variation in the amount of leaf lamina between sorophores (Halle, 1940: pl. 1, figs 4-8). *Lygodium dinmorphyllum* pinnae from Dinmore exhibit similar ranges of variation (Fig. 4) with some fertile pinnae 'free' of lamina, and others bearing extensive laminae between the sorophores (Churchill, 1969: fig. 2). In most of the Golden Grove, Maslin Bay and Anglesea material the fertile pinnae are nonlaminar. Fertile pinnae of *L. kaulfussi* are also nonlaminar although pinnules intermediate in character between sterile and fertile pinnules are preserved (Manchester & Zavada, 1987: fig. 8). The sorophores attached to the sterile pinnule from Dinmore can similarly be explained as a 'leaflet' intermediate in character between sterile and fertile pinnules (Fig. 4E-F). The annulus on the sporangia is not preserved in material from any site. Halle (1940) and Manchester & Zavada (1987) noted that the annulus could not be discerned in *L. skottsbergii* and *L. kaulfussi* respectively.

Spore Morphology

Spores from complete sorophores of *L. dinmorphyllum* are known from Anglesea (Douglas, 1978) and have been extracted from Golden Grove material. The spores broadly resemble those from fossil *Lygodium* (excluding *L. poolensis* Chandler, 1955) described from the Northern Hemisphere (Buzek & Konzalová, 1983; Chandler, 1955; Manchester & Zavada, 1987). Although spores were recovered from *L. dinmorphyllum* from a number of sites the best preservation is in the Golden Grove material and descriptions are based on this material. In general, the spores possess a subtriangular amb with convex to straight (occasionally concave) interradials and rounded radials. The laesura are slightly sinuous, often open and gaping, and extend two thirds of spore radius towards the amb. The laesura are bordered by labra 5-7μm wide and raised 6-8μm. Spore exine is approximately 2μm thick and thickened in the radial areas to 5μm. Ornamentation is best developed on the distal surface and comprises low verruca, short rugula and low sinuous to bifurcating ridges enclosing short irregular lumina; ornamentation is reduced on the proximal surface, particularly in the proximal polar area (Fig. 10). In optical section the amb is gently undulating. Some specimens appear to bear remnants of an irregular perisporum. Based upon measurements from 15 specimens the equatorial diameter of the spores is 67 (82) 95μm and polar diameter is 59 (75) 90μm.

The spores from *L. dinmorphyllum* sorophores are identical to the form species *Cyathidites splendens* Harris, 1965. The holotype of *C. splendens* was examined but the mounting medium and spore are too dehydrated to provide useful morphological information and comparisons were limited to photographs and published descriptions. However free spores of *C. splendens* occur consistently in the Golden Grove and Maslin Bay carbonaceous lenses as well as other Australian early Tertiary sediments (Fig. 10). *Cyathidites splendens* has also recently being recognized in Late Cretaceous (Maastrichtian) sediments from the offshore Bight and Duntroon Basins, off South and Western Australia (NA, pers. obs). Spores of the form species *C. gigantis* (Cookson) Harris, 1965 also bear some similarity to the spores extracted from the *L. dinmorphyllum* sorophores. However the holotype of *C. gigantis* and other free spores from early Tertiary sediments were examined and found to be smaller, possess a much thickened exine with prominently thickened radials, and coarse ornamentation in the proximal polar area, diminishing greatly in the equatorial interradial areas. The *L. dinmorphyllum* spores therefore correlate with the form species *C. splendens* Harris, 1965.

Cuticle Morphology

Attempts to prepare cuticle from the mummified Golden Grove leaves have proved difficult but small fragments were obtained. *Lygodium dinmorphyllum* pinnules from Golden Grove are probably hypostomatic as is modern *L. articulatum*. The stomata of *L. dinmorphyllum* from Golden Grove are anomocytic, as in extant *Lygodium* (Clifford & Constantine, 1980) and the anticlinal epidermal walls are strongly sinuous (Fig. 11 F,H). The stomata appear to be irregularly oriented on the leaf surface as in modern *L. articulatum* (Fig. 11D). SEM micrographs of impressions of Dinmore material also demonstrate sinuous anticlinal epidermal walls but stomata are not evident (Fig. 11 A,B). *Lygodium kaulfussi* has sinuous anticlinal epidermal walls and stomata comparable in size to those of *L. dinmorphyllum*. Unlike *L. dinmorphyllum* the stomata in *L. kaul-*

fussi are diacytic, arranged in rows and the anticlinal epidermal walls are not as strongly sinuous (Kräusel & Weyland, 1950). The stomata in *L. kaulfussi* are oriented between two epidermal cells, while in *L. dinmorphyllum* the stomata are surrounded by four or five cells.

The cuticle of *L. dinmorphyllum* sorophores indicates that the anticlinal epidermal walls are sinuous but not to the same extent as the leaves (Fig. 11G). No stomata were seen.

CONCLUSION

Even with ample material as provided by the Golden Grove and Dinmore localities, species assessment is difficult, as the material is extremely variable. The limited material from Cethana or Temuka is therefore difficult to interpret particularly with only photographic evidence available. Similarly early records of *Lygodium* (such as Ettingshausen, 1886, 1888), which are based solely on sterile foliage are also not presently resolvable. Northern Hemisphere species based on limited material present similar problems as Manchester & Zavada (1987) have shown.

Palaeobiogeographical speculation on the radiation and evolution of *Lygodium* is difficult because of the cosmopolitan distribution and extensive Tertiary fossil record (Kräusel & Weyland, 1950; Reed, 1947). The extensive fossil record of *Lygodium* in Australia suggests that the extant Australian species may be derived from these early Tertiary forms. However, as fossil *Lygodium* is also known from the Miocene Notonakajima flora of Japan and Oligocene floras of Manchuria (Matsuo, 1963; Florin, 1922) it is equally possible that the modern northern Australian species *L. japonicum*, *L. flexuosum*, *L. microphyllum* and *L. reticulatum* are recent arrivals from Asia as Page & Clifford (1981) speculated. These species are all widely distributed within the Malesian region (Holttum, 1959). The weakly dimorphic fertile foliage of most of the Malesian species, i.e. the fertile pinnules resemble the sterile pinnules, suggests a closer affinity to *L. mioscandens* Matsuo(1963) from Japan than with the fossil material from the early Tertiary of Australia. Manchester & Zavada (1987) suggested that species with lamina surrounding the sorophores, e.g. *L. japonicum* and *L. flexuosum* are relatively recent in origin. The high diversity of *Lygodium* species in the Malesian area may be due to a relatively recent and rapid speciation and radiation in this region. This may explain, in part, Holttum's (1959: 39) difficulties in defining modern species within the genus.

Cyathidites splendens ranges from the Late Cretaceous through to the Pliocene in southern Australia. In the early Tertiary Eyre Formation of the Lake Eyre Basin *C. splendens* is common and can be locally more frequent in parts of the Paleocene section. The frequency of the spore in palynomorph assemblages, however, decreases through the Tertiary and *C. splendens* is rare in Pliocene assemblages. *Cyathidites splendens* is commonly associated with palynofloral assemblages that are indicative of rainforest communities. The gradual decrease in the frequency of *C. splendens* through the Tertiary in southern Australia may be related to the overall decline in temperature and precipitation during this interval.

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APPENDIX A
LYGODIUM MATERIAL EXAMINED
(F=fertile. S=sterile)

Dinmore, Redbank Plains Formation, SE Qld
QMF2857-8 (S); QMF12544 (F); QMF13464 (S); QMF14096 (S); QMF14360 (S); QMF14361 (S/F); QMF14362-3 (S); QMF14365-7 (S); QMF14464-7 (F); QMF14530 (F); QMF15809 (S); QMF14924 (F); QMF14974 (S); QMF15314 (S); QMF15317 (F); QMF15318-9 (S); QMF15320-1 (S); QMF18035 (S); QMF18904 (S). UQF10620 (F); UQF10720 (F); UQF10726 (S); UQF12450-1 (F); UQF32006 (S). GSQF12973 (F); GSQF12974 (S); NMVP26688 (F) Holotype, *L. dinmorphyllum*; NMVP26689 (F) Paratype, *L. dinmorphyllum.*

Cethana, Tasmania
UTC232 (S); UTC235 (S).

Vegetable Creek, N.S.W.
GNSWF8820 (S), Holotype, *L. strzeleckii.*

Maslin Bay, North Maslin Sands, S.A.
UAS715-6 (S); UAS1211 (S); UAS1868 (S); UAS2274 (S); UAS2513-4 (S); UAS2691-2 (S); UAS3502 (S); UAS3524 (F); UAS3537-8 (S); UAS3546-7 (S).

Golden Grove, North Maslin Sands, S.A.
UAG1379 (S); UAG1398 (S); UAG1400 (S); UAG2604-5 (S); UAG2607-8 (S); UAG2718 (S); UAG2720 (S); UAG3001-26(S); UAG3036-42 (F).

Anglesea, Eastern View Coal Measures, Victoria
NMVP165681 (F); NMVP178144-9 (S); NMVP178150 (F).

Temuka, New Zealand
NZGSB25/90-92.

BRYOZOA FROM HERON ISLAND, GREAT BARRIER REEF

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Eighty-one species of Bryozoa are described from shallow reef habitats around Heron Island, Queensland. Fourteen new species are described: *Puellina decipiens, P. egretta, P. vulgaris, Celleporaria desperabilis, Robertsonidra novella, Parasmittina galerita, P. onychorrhyncha, P. turbula, Pleurocodonellina clavicula, Microporella fimbriata, Celleporina reginae, Rhynchozoon ardeolum, R. limatulum* and *R. scopulorum*. Twenty four species are recorded for the first time from Australian waters. □*Heron Island, Great Barrier Reef, Bryozoa, taxonomy, new species.*

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The coral-associated bryozoan fauna of the Great Barrier Reef (GBR) is undoubtedly very diverse, probably comprising several hundred species. It is, however, poorly known. Thus, in the late 19th century, when the rich bryozoan fauna of Victoria and, to a slightly lesser degree, of New South Wales and South Australia, was being described, the GBR bryozoans were known only by a few specimens from HMS Rattlesnake (Busk, 1852a), from Port Denison and Holbourne Island (Haswell, 1881) and from A.C. Haddon's collections in Torres Strait (Kirkpatrick, 1890a). This lack of study continued through most of the 20th century, with coastal Queensland or GBR bryozoans being described in only a few short papers (Livingstone, 1926; Hastings, 1932; Silén, 1942; Ross, 1974; Ryland, 1974, 1984) and lists (Livingstone, 1927; Dall & Stephenson, 1953; Hall, 1984; Winston, 1986). Consequently, the view prevailed that bryozoans were poorly represented in coral reefs generally and in the GBR particularly (Ryland, 1974). That this must have been erroneous was evident from Maxwell's (1968) study of sediments in which bryozoan fragments, representing a wide diversity of species, formed an important constituent. Recent semi-popular descriptions of the GBR have been given by Bennett (1971), Endean (1982) and Talbot (1984), providing useful background information on the fauna generally but little on the Bryozoa specifically.

The GBR is extensive, stretching some 1900km from Lady Elliot Reef (24°07'S), slightly south of the Tropic of Capricorn, to the Warrior Reefs and Bramble Cay in the Gulf of Papua (9°09'S). The reefs are dispersed over, and along the edge of, the continental shelf and occupy an area of some 215,000km^2. It is to be expected that the bryozoan fauna will vary with latitude and, most species being essentially subtidal, would be appropriately studied and collected by scuba. The present contribution, in which we describe 81 species, is manifestly preliminary being based on a still incomplete examination of specimens collected intertidally on Heron Island reef, one of the southernmost in the GBR, mainly over a few days in 1972.

Heron Reef is one of 16 comprising the Capricorn Group which, together with four of the Bunker Group, lie between latitudes 23° and 24°S, at the southern end of the GBR. These reefs are separated from Breaksea Spit (Sandy Cape) to the southeast and from the mainland coast in the neighbourhood of Gladstone by Curtis Channel, while the Swain Reefs lie about 150km northwards across the Capricorn Channel. The 200m isobath lies some 16-25km east of the Capricorn Group, whilst the mainland is about 70km to the southwest. A map of the group, with bathymetry, is given by Jell & Flood (1977) and Mather & Bennett (1984).

Mean water temperatures are 26-27°C in summer dropping to 20-21°C in winter, but temperatures over the reef flat may exceed 32°C or drop to 17°C, or even lower (Endean et al., 1956). Prevailing winds are southeasterly, or from between southeast and east during summer. Low-amplitude ocean swells thus approach predominantly from roughly the southeast. The East Australian Current outside the shelf edge flows polewards but there is little information on the current patterns within the southern GBR. In the central GBR the residual flows are determined by prevailing winds, setting northerly

during periods of steady tradewinds but southerly during light or variable breezes (Wolanski & Pickard, 1985). Releases of surface drifters in the Capricorn Channel suggested a nett southerly movement (Woodhead, 1970). Tides are semi-diurnal, though successive tides frequently differ in height; mean amplitudes are 2m on springs and 1m on neaps. Tidal currents set westerly on the flood, easterly on the ebb.

Heron Island, the cay (23°27'S, 151°55'E), is situated at the leeward (western) end of an egg-shaped lagoonal platform reef (Jell & Flood, 1977), roughly 8.5 by 4km with the long axis orientated ESE-WNW (Fig. 1). At its eastern end, Heron Reef is separated from the smaller Sykes Reef, with which it shares a reefal platform, by a 3km wide channel of about 15m depth (map in Jell & Flood, 1977). The southwestern quarter of Heron Reef is separated by a channel, about 700m wide and 30m deep, from Wistari Reef. The disposition of the two reefs ensures that the western extremity of Heron Reef, and especially the northern aspect of it, is well sheltered from direct impact of the tradewind swells, although waves from the southeast are refracted around the reef. Wave-transported particles are deposited in the vicinity of the cay (Flood, 1974). During the ebb, water from the reef drains in a radial manner (except near the boat channel, see below) until the rim becomes exposed. A shallow lagoon occupies the east-central area of the reef. At spring tides there is an extensive peripheral reef flat, especially at the western end, covered by 0.5m of water or less. The edge of the reef is then accessible from the cay by wading. Access to other parts of the reef edge at low tide, and to the drop off for scuba, must be by boat.

Most descriptions of Heron Island refer more to the cay than to the reef (e.g. Steers, 1938) but brief accounts of the reef have been given by Endean et al. (1956), Cribb (1966), Jell & Flood (1977) and Mather & Bennett (1984). Important man-made features are the boat channel and the cay's western retaining wall. Marine engineering works up to 1980 were summarized by Gourlay & Flood (1981), with particular reference to the stability of the cay, although there have been consequences on the reef flat to the south of the cay. In 1945 a gap was blasted in the reef rim, opposite the northern tip of Wistari Reef, to provide access for small boats. A wreck (still there) was positioned to provide shelter. The gap was extended in 1966-67 to provide a dredged boat channel and harbour. The channel has subsequently been filled with sand mobilized by cyclones, e.g. 'Emily' (Apr 1972), 'David' (Jan 1976) and 'Simon' (Feb 1980), each time being dredged clear afterwards. The boat channel was extended in 1987-88 (Flood, 1989) and is now associated with a long and substantial jetty. These developments have affected sediment deposition (Gourlay & Flood, 1981), a symptom of a substantially altered flow regime over the southern cay-side flat. Most of the Bryozoa described in this paper were collected from this area in 1972. Water no longer drains radially from the reef here but (1988) flows strongly along the flat towards the channel. The reef flat provided a rich collecting area in 1972 but seemed to have deteriorated markedly by 1988, even before the consequences of the 1986-87 developments (already apparent on water flow) could have affected the living coral framework.

The reef flat extends seawards from the cay to the inner side of the reef rim. At low water springs, away from the boat harbour, water drains through gaps and channels in the rim, but the flat never wholly dries. The inner part of the flat is largely sandy, with patches of coral rubble and some living coral, e.g. *Porites cylindrica*. The outer flat is characterized by living coral, extensive development of crustose coralline algae, and drifts of coral shingle; sand is restricted to small pools and narrow channels. In 1972 the flat at the western end (beyond the boat harbour) was extensively carpeted with a level forest of *Acropora* but shingle has increasingly accumulated since then.

The reef rim is higher than the upper level of live coral on the outer flat. Its surface is cemented with crustose coralline algae, and zoanthids (especially *Palythoa* spp.) are conspicuous. Coral shingle, coral boulders (derived from *Acropora hyacinthus* heads), and sometimes large blocks derived from bommies (plate 30B in Saville-Kent, 1893), accumulate on and just inside the rim. While the rim pavement is devoid of habitats suitable for bryozoans, the boulders constitute the richest intertidal habitat for them.

The reef slope is the sublittoral extension of the reef rim. On the windward (southeastern to southwestern) side of the reef, the upper slope has spur and groove form and the gradient varies from 1 in 20 in the southeast to 1 in 4 southwest of the cay (Jell & Flood, 1977). When accessible in calm weather the coral growing on the spurs would undoubtedly prove a rich habitat for Bryozoa. On the lee side of the reef the spur and groove formation does not develop; rather there is extensive growth of tabular corals, such as *Acropora hyacinthus*. In 1972 some bryozoans

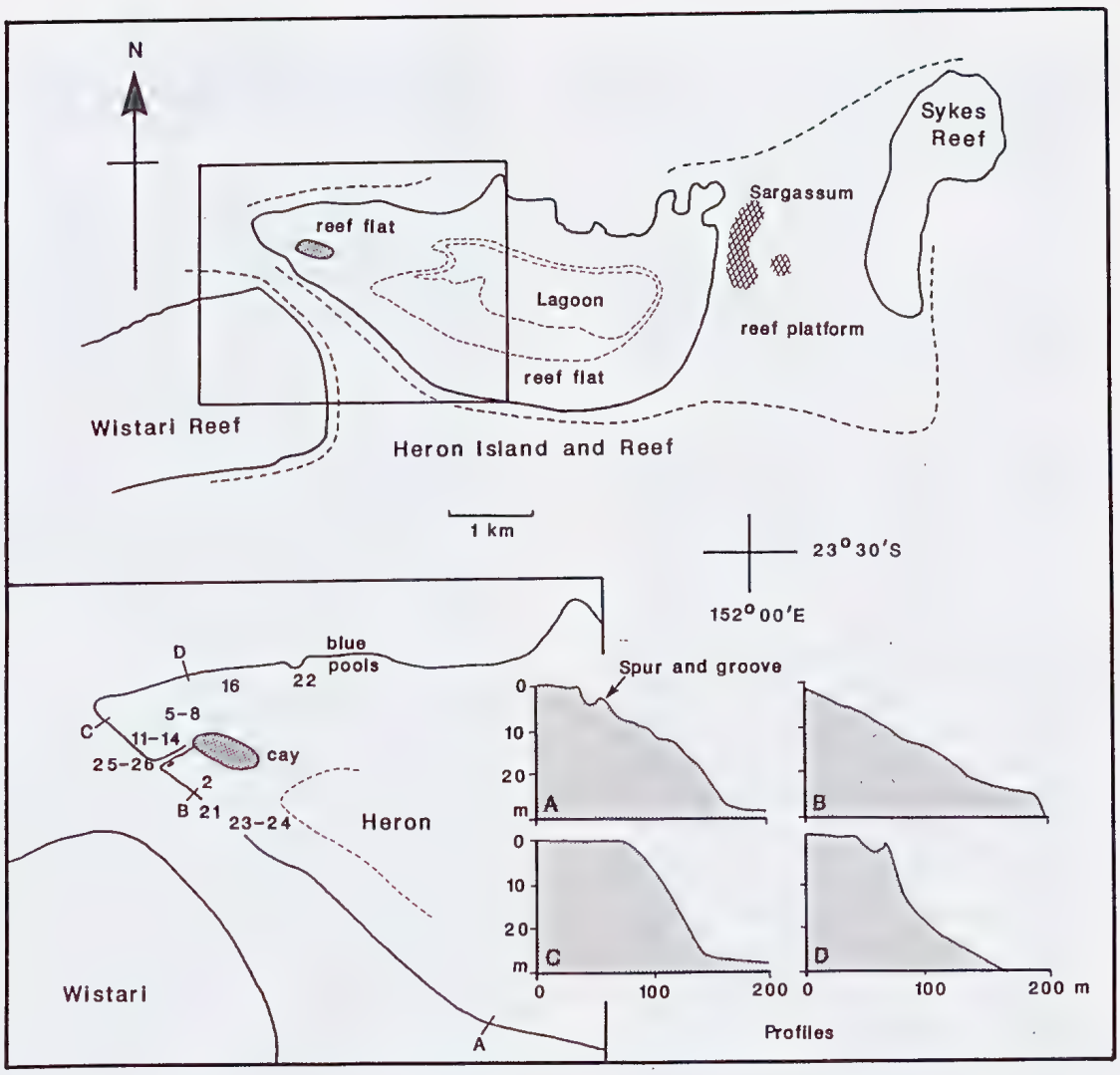


FIG. 1. Heron Island and Reef, showing location of samples. Profiles from Jell & Flood (1977).

were collected by snorkelling and scuba from under such tables, and photographs show the richness there of sessile fauna. It is such tables that, when struck by tropical cyclones, are broken free and hurled onto the edge of the reef. They ultimately settle in the only stable position, with the former attachment facing upwards. The cryptic surface is usually somewhat concave, such that the boulder rests on its rim; irregularities ensure that water circulates through the space, keeping the boulder surface clear of sediment. In this dark, protected habitat ascidians, bryozoans and sponges develop in profusion. Thus the boulders in the Blue Pools area, north of the cay, which were deposited by cyclone 'Emily' (Apr 1972), by 1988 had developed an abundant and colourful sessile fauna of great diversity.

In 1988 occasional pieces of drift *Sargassum* heavily colonized with bryozoans such as *Aetea, Crisia, Lichenopora* and *Membranipora* and hydroids *Eudendrium* and *Plumularia* were collected on the beach of the cay. At the time it was not known where the *Sargassum* was growing. Subsequently, a bed of *Sargassum* has been located by Lin Baldock and Myriam Preker in 10-15m water in the channel between Heron and Sykes reefs. The species here differ from those of boulders and discovery of the *Sargassum* bed should greatly benefit future studies on the Bryozoa.

MATERIALS

With the exception of two species of *Bugula* found on boulders near Blue Pools in 1988, the bryozoans described in this paper are from 14 of the 28 samples obtained by JSR in 1972. These are identified by sample numbers (Fig. 1) as follows:

2. 9 Apr, 1972. On the reef flat south of the cay. Bryozoa were collected on pieces chipped off tabular *Acropora*, in situ, or from dislodged heads resting on the sand. Bryozoans were present on under surfaces, though rarely abundant, and less common than sponges.
5. 11 Apr, 1972. On the reef flat WNW of the cay. Flat plates of coral, the outer parts spread as horizontal laminae, the inner were convoluted, forming recesses and clefts sheltering *Margaretta*, lace corals (Phidoloporidae), and cellularines.
6. 11 Apr, 1972. Near 5 on the reef flat WNW of the cay. Plates of *Echinopora* with encrusting bryozoans on the lower surface.
8. 11 Apr, 1972. Near 5 and 6. The flat here was a level platform of abraded *Acropora* with a maze of cavities underneath, and coral 'fingers' rising from the surface. The encrusting fauna seemed poorer than under individual tables.
11. 12 Apr, 1972. On the reef flat west of the cay, to the north of the boat channel. Part of a well-developed *Acropora* head which had tipped when stepped on. The outer parts were coated with a thin, filmy prussian blue sponge. Several *Reteporella graeffei* and incrusting species were present.
12. 12 Apr, 1972. On the reef flat, near 11. Below the actively growing *Acropora* head, supported by a slender pedestal, was a layer representing an earlier growth level, 3-5cm thick, with sediment lying on its upper surface. The lower surface was white, lacking encrusting coralline algae, but bearing *Tubastrea*, sponges, *Filograna*, a brachiopod, and bryozoans. Below this was coral rubble.
14. 12 Apr, 1972. Near 12. Pieces broken from a large *Acropora* head which had become free and turned upside down, though continuing to grow.
16. 13 Apr, 1972. Crest to the west of the cleft in the reef edge, northeast of the cay. The crest here was strewn with boulders deposited (or redistributed) by cyclone 'Emily' (1-2 Apr). The sessile fauna on the *Acropora* was protected by the knobbly surface of the pedestal. Fragments of typically subtidal erect Bryozoa, such as *Triphyllozoon* and violet *Iodictyum*, were also picked up here. (These boulders were examined in 1988, having been on the reef for 16 years. The fauna is still being studied).
21. 14 Apr, 1972. Reef crest south of the cay. Most of the flat approaching the crest at this point was level, easy to walk on, rather than being a forest of heads. Several coral boulders derived from *Acropora* heads were present. The living coral of the crest tended to form layers (almost shelves). While water on the flat appeared to ebb over the coral, on the crest it noticeably percolated through the coral. The space matrix would seem ideal for bryozoans being fairly dark and with long periods of water flow. The coral heads typically, though not invariably, displayed a lower surface zonation, with the peripheral fingers covered with lithothammion and the centre region white, with *Filograna* tubes, sponges, compound ascidians and Bryozoa. The sample was a piece of boulder showing a coral/bryozoan interface.
22. 15 Apr, 1972. Reef crest at the cleft, northeast of the cay. The crest here is more complex than at 21. There is the actual edge, marked by surf, then a moat; the coral then rises onto the crest which merges into the zone of coral boulders and rubble (see profile D, fig. 1, from Jell & Flood, 1977). Along the crest coral was dying back, apparently because cyclone 'Emily' had altered the drainage pattern, leaving the coral heads dry and dying; or live coral had been flattened by pounding with the *Acropora* boulders produced by the cyclone. Sample was from these boulders, though most *Iodictyum* fragments were unattached.
23. 16 Apr, 1972. Reef crest south of the cay; collection made by turning boulders. Tide poor; reef edge not exposed; water running off the reef as a sheet.
24. 17 Apr, 1972. Near 23; from well-incrusted boulders.
25. 18 Apr, 1972. Collection from 4.5-9m at bommie made by D.R. Robertson. Included *Bugula dentata, Nellia simplex* and Phidoloporidae.
26. 18 Apr, 1972. Near 25, about 3m depth on the slope.

Holotypes and paratypes of the new species described here are in the Queensland Museum.

ACKNOWLEDGEMENTS

We are grateful to the Nuffield Foundation for the provision of a Travelling Fellowship to JSR in 1971/72, to the Royal Society for a travel grant in 1988, and to the Australian Biological Resources Survey for generous financial support for our research. Thanks are also due to the Director of the Heron Island Research Station, Dr Ian Lawn, and to Miriam Preker, who kindly supplied data on the distribution of *Sargassum*, and Dr P.G. Flood for freely given advice and information on the physical environment of Heron Island. P.J. Chimonides and Mary E Spencer-Jones (Natural History Museum, London) were most helpful in facilitating the loan of type specimens. Dr M.R. Fordy (School of Biological Sciences, University of Wales, Swansea) is especially thanked for his valued expertise in scanning electron micrography.

SYSTEMATIC ACCOUNTS

The taxonomic order adopted here follows that established by Gordon (1984, 1986, 1989b). Taxonomic diagnoses are provided at family and genus level, and the species descriptions and measurements are based on Heron Island specimens. The synonymies given for each species are deliberately selective, being limited to the original description and the most useful, recent accounts. Unverified synonymies have been avoided. The occurrence of each species at Heron Island, and its wider geographical distribution, are briefly noted. It is intended that a more precise account of the ecological distribution of the bryozoan fauna will be prepared after the completion of the present, continuing research project.

Class STENOLAEMATA Borg, 1926
Order CYCLOSTOMIDA Busk, 1852a
Family LICHENOPORIDAE Smitt, 1867

Colony encrusting, regularly circular or oval, occasionally developing as a cylinder around erect substrata; concave or domed, nodular or mamillate, often lobed; bordered by a peripheral lamina of common basal wall. Autozooids radiating from centre of colony, sometimes in irregular quincuncial series, more usually in connate, uniserial or multiserial rows. Extrazooidal space between zooid rows divided by calcified struts, defining polygonal spaces referred to as alveoli. Brood chambers originating in centre of colony, with lobes extending between zooid rows, roofed by finely granular calcification; ooeciostomes situated at edges of brood chamber, between zooid rows.

Lichenopora Defrance, 1823

With the characters of the family.

Type species: *Lichenopora turbinata* Defrance, 1823.

Lichenopora novaezelandiae (Busk)
(Fig. 2a,b)

Discoporella novaezelandiae Busk, 1875: 32, pl. 30, fig. 2.

Lichenopora novaezelandiae: Brood, 1976: 299, figs 17A-C (not figs 17G-I, = *Disporella sibogae* Borg); Hayward & Cook, 1983: 137.

DESCRIPTION

L. novaezelandiae, as described and figured by Busk (1875) and Harmer (1915), has uniserial zooid rows and a simple, rounded ooeciostome. Brood (1976) appears to have confused his figures with those of *Disporella sibogae*, a superficially similar species in which the zooid rows are always biserial. Colonies are typically oval and domed, and may reach 10mm in length. This species is probably quite common in shallow reef environments, but it is generally inconspicuous. Several large colonies were present in the interstices of *Acropora* in sample 2.

DISTRIBUTION

It is distributed throughout the western Pacific, from New Zealand to Japan, and westwards to the east coast of Africa.

Class GYMNOLAEMATA Allman, 1856
Order CHEILOSTOMIDA Busk, 1852a
Suborder ANASCINA Levinsen, 1909
Superfamily MEMBRANIPOROIDEA Busk, 1854
Family CALLOPORIDAE Norman, 1903

Colony encrusting, forming coherent or disjunct sheets, or reticulate to uniserial runners; or erect, developing bilaminar plates or arborescent, vinculariiform growths, attached by an encrusting base. Frontal wall of autozooids with extensive membrane, sometimes overarched by spines but always conspicuous; gymnocystal and/or cryptocystal calcification usually present, often well developed. Spines present or absent.

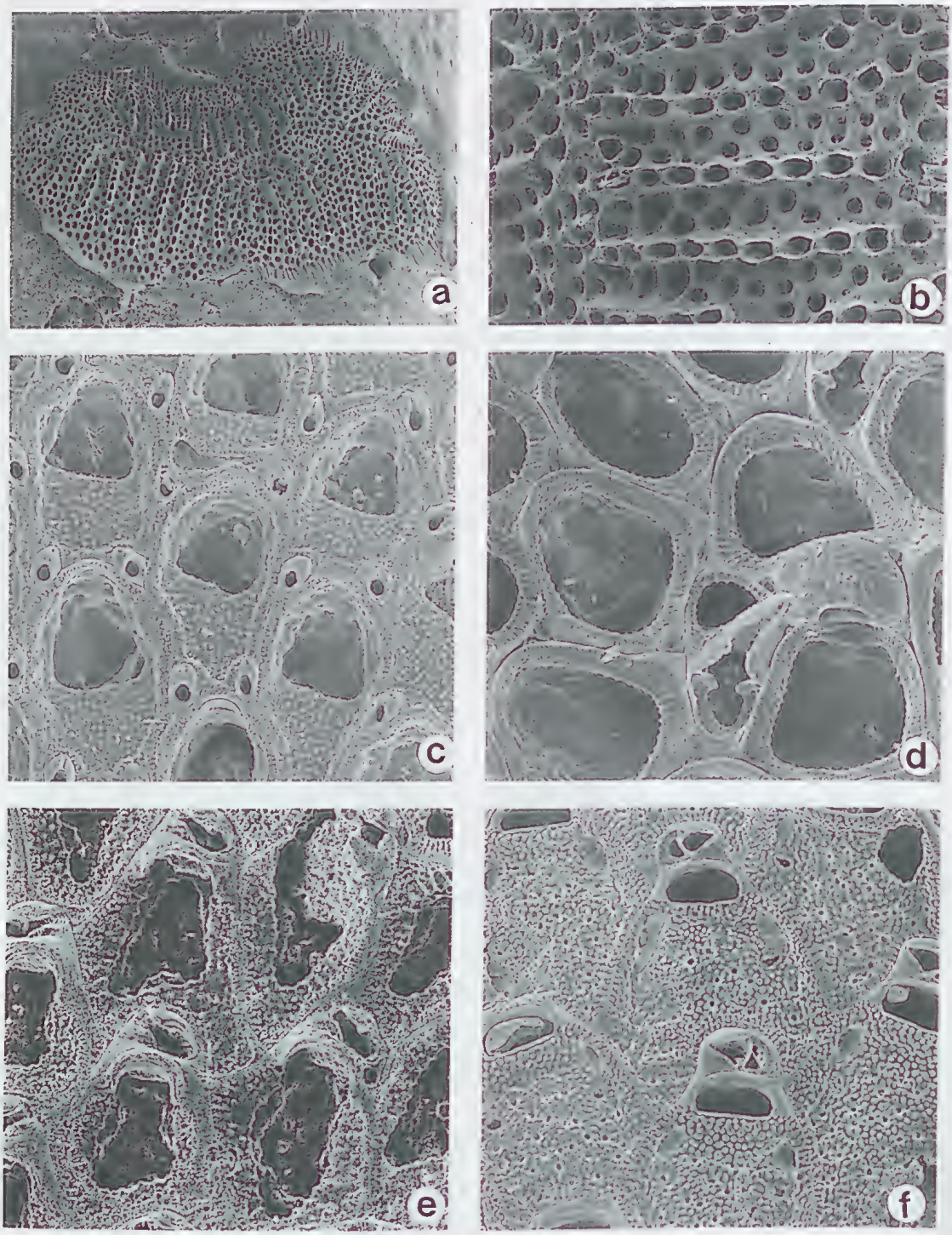


FIG. 2. a,b, *Lichenopora novaezelandiae*; a, whole colony, ×9; b, detail showing oeciostome between two zooid rows, ×30. c, *Antropora granulifera*, ×80. d, *Parellisina curvirostris*, ×60. e, *Cranosina coronata*, ×50. f, *Micropora variperforata*, ×75.

Avicularia adventitious and/or vicarious, sometimes lacking. Ovicells generally present, hyperstomial, or partly immersed, reduced. Vertical walls with large basal pore chambers, or mural septula.

Antropora Norman, 1903

Colony encrusting. Autozooids with well developed cryptocyst; gymnocyst negligible or absent. No spines. Avicularia interzooidal, small, sometimes lacking. Ovicell endozooidal, its presence indicated by a slight thickening at the distal end of the autozooid. Basal pore chambers present.

Type species: *Membranipora granulifera* Hincks, 1880b.

Antropora granulifera (Hincks) (Fig. 2c)

Membranipora granulifera Hincks, 1880b: 72, pl. 9, fig. 4.
Antropora granulifera: Harmer, 1926: 232, pl. 14, figs 11-14; Cook 1968a: 138, text-fig. 9.

DESCRIPTION

Colony forming flat, unilaminar sheets. Autozooids irregularly oval to hexagonal, each with a raised crenellated rim; 0.4-0.5×0.2-0.3mm. Cryptocyst occupying about half total autozooid length, flat or slightly concave, coarsely beaded; opesia subtriangular. At the distal end of each autozooid is a pair (rarely one) of small, interzooidal avicularia, each budded from a disto-lateral pore chamber; rostrum acute to frontal plane, directed distally or disto-medially, 0.07mm long, with a short triangular mandible.

DISTRIBUTION

Antropora granulifera is possibly circumtropical in distribution. It has been reported from Madeira, West Africa, Sri Lanka, Indonesia and the tropical eastern Pacific, but has not been recorded previously from the Great Barrier Reef. It was found at two stations on Heron Island (samples 2 and 16), on the reef flat to the south of the cay, and on the reef edge to the northeast.

Parellisina Osburn, 1940

Colony encrusting. Autozooid with narrow cryptocystal rim, and minimal area of gymnocyst. Spines reduced or absent. Avicularia vicarious, large, each associated with a small kenozooid. Ovicell prominent, hyperstomial. Basal pore chambers present.

Type species: *Membranipora curvirostris* Hincks, 1862.

Parellisina curvirostris (Hincks) (Fig. 2d)

Membranipora curvirostris Hincks, 1862: 29; 1880a: 153, pl. 20, figs 5,6.
Ellisina curvirostris: Harmer, 1926: 228, pl.14, fig. 7.
Parellisina curvirostris: Cook, 1968a: 156, text-fig. 16; Winston, 1984: 7, fig. 14; Winston & Heimberg, 1986: 6, figs 7,8.

DESCRIPTION

Colony forming small, unilaminar patches. Autozooids broadly oval or pear-shaped, commonly 0.5×0.3mm, the extensive frontal membrane bordered by a raised mural rim; a pair of delicate, evanescent, distal oral spines present in early ontogeny. Avicularia frequent; distinctive: rostrum acute to frontal plane, 0.25mm long, laterally curved; associated with a kenozooidal polymorph, with a rounded opesia, visible distal to the rostrum. Ovicell relatively small, the ectooecium membranous frontally, exposing granular entooecium.

DISTRIBUTION

This familiar species has a pantropical distribution, ranging into temperate regions in the north-east Atlantic and perhaps elsewhere. It forms small, and generally inconspicuous, colonies on hard substrata, particularly biogenic carbonates. It is common at Heron Island, occurring in seven of the sample stations reported here.

Crassimarginatella Canu, 1900

Colony encrusting; or erect, attached by an encrusting base, bilaminar or vincullariiform. Autozooids with extensive opesia, bordered by a narrow, granular cryptocyst; gymnocyst variably developed. Spines present or absent. Avicularia vicarious. Ovicell prominent, hyperstomial, or small and cap-like. Vertical walls with basal pore chambers or mural septula.

Type species: *Membranipora crassimarginata* Hincks, 1880b.

Subgenus **Corbulella** Gordon, 1984

Autozooids with well developed gymnocyst, and numerous marginal spines.. Avicularia

vicarious, with proximal opesia bordered by spines. Ovicell prominent, hyperstomial, with a broad frontal fenestra.

Type species: *Membranipora corbula* Hincks, 1880c.

Crassimarginatella (Corbulella) corbula (Hincks) (Fig. 3)

Membranipora corbula Hincks, 1880c: 378, pl. 17, fig. 6.

Crassimarginatella (Corbulella) corbula: Gordon, 1984: 29, pl. 3, figs D,E; 1986: 32, pl. 5, fig. A.

DESCRIPTION

Colony encrusting, forming a small, flat, unilaminar sheet. Autozooids oval, 0.5× 0.35mm, with large oval opesia, a narrow, granular cryptocyst and a reduced, smooth gymnocyst. Twelve to 18 pairs of spines distributed around the opesia, the distal one or two pairs stout, erect, the rest thin, incurved over the frontal membrane. Ovicell spherical, with a transversely oval frontal fenestra, its distal edge often developing a short umbo. Avicularium slightly larger than autozooids, its distal half comprising a raised, smooth-edged rostrum, supporting a semielliptical mandible; proximal half consisting of a shortened opesia bordered by three or four pairs of curved spines.

DISTRIBUTION

This species is widely distributed in the western Pacific from Japan to New Zealand. A single colony was present in sample 16, from the reef edge northeast of the cay.

Cranosina Canu & Bassler, 1933

Colony encrusting. Frontal membrane of autozooid underlain by a broad, peripheral cryptocyst; gymnocyst absent. No spines. Avicularia interzooidal, typically one budded from each autozooid; mandible setiform. Ovicell reduced, endozooidal, or lacking. Large basal pore-chambers present.

Type species: *Membranipora coronata* Hincks, 1881a.

Cranosina coronata (Hincks) (Fig. 2e)

Membranipora coronata Hincks, 1881a: 147, pl. 10, fig. 1.

FIG. 3. *Crassimarginatella (Corbulella) corbula.*

Cranosina coronata: Winston & Heimberg, 1986: 6, figs 3-6; Hayward, 1988: 281.

DESCRIPTION

Colony forming flat, unilaminar sheets. Autozooids irregularly oval to hexagonal, separated by distinct grooves; 0.65-0.7×c.0.4mm. Cryptocyst coarsely beaded, the beads aligned in ridges, directed medially and imparting a crenulate edge to the cryptocyst. Distal end of autozooid raised, with a hood-like border of smooth, gymnocystal calcification supporting the operculum. Avicularium developed from the distal pore chamber of each autozooid, its cystid not clearly distinguishable from the distal wall of the autozooid; rostrum transversely orientated, at a slight angle to the frontal plane, constricted medially, its distal end flared; mandible setiform, very finely toothed, about 0.4mm long.

DISTRIBUTION

A single small colony of this species was present in sample 16. It is distributed throughout the Indo-West-Pacific region, from the Philippines to Sri Lanka and Mauritius. Also reported

from Puerto Rico (Osburn, 1940) and Venezuela (Winston, 1986).

Family QUADRICELLARIIDAE Gordon, 1984

Colony erect, branching, jointed. Autozooids elongate, opesiae extensive; cryptocyst moderately to well developed; gymnocyst reduced. Avicularia adventitious, or absent. Ovicells present or absent. Ancestrula resembling later autozooids, but with a tubular proximal portion rising from an uncalcified stem.

Nellia Busk, 1852b

Colony erect, branching, jointed; internodes square-sectioned, consisting of four longitudinal series of autozooids, arranged in alternating, back-to-back pairs. Autozooids with well-developed gymnocyst; opesia with broad, proximal border of cryptocyst and surrounded by raised mural rim. No spines. Avicularia adventitious. Ovicells small, partly immersed.

Type species: *Nellia oculata* Busk, 1852b.

Nellia tenuis Harmer
(Fig. 10c)

Nellia tenuis Harmer, 1926: 245, pl. 14, figs 16-17.
Nellia tenuis Hayward, 1988: 286, pl. 1, fig. a; Gordon, 1989a: 450, fig. 3.

DESCRIPTION

Colony delicate, inconspicuous, formed from internodes 1-4mm long, 0.25mm wide; dividing dichotomously at infrequent intervals, most often developing simply an undivided series of two or three internodes. Joints between internodes consisting of slender, cuticular tubes; each internode finely tapered proximally. Autozooids about 0.5×0.25mm, the narrow, oval opesia comprising about three-fifths of total autozooid length. A pair of avicularia at the distal end of each autozooid; rostra pointed, hooked, at right angles to long axis of internode.

DISTRIBUTION

Nellia tenuis is probably quite common in shallow reefal habitats. At Heron Island, it was present in samples 14 and 24, from the reef flat west of the cay, and the reef crest to the south. Harmer (1926) had fragmentary specimens from three localities in the Indo-Malaysian region, and listed a fourth from the South China Sea. Ryland (1984) illustrated specimens from Fiji. It was abundant on Mauritian reefs, as part of a bryozoan sward developed beneath coral boulders (Hayward, 1988).

Superfamily BUGULOIDEA Gray, 1848
Family BUGULIDAE Gray, 1848

Colony erect and branched, unjointed, unilaminar, attached by rhizoids. Zooids long, parallel-sided, with almost all of the frontal surface membranous; lateral walls lightly calcified; marginal spines usually present. Pedunculate 'bird's head' avicularia characteristically present. Ovicells independent and hyperstomial, with the ectooecium membranous.

Bugula Oken, 1815

Colony erect, growing from an upright ancestrula, branching; attached by rhizoids which issue from frontal, lateral and basal surfaces of the autozooids. The latter arranged in two or more series, alternating; boat-shaped, with the proximal end forked and the distal end of the next lowest zooid wedged into the fork, extending beyond it on the frontal side; with a row of uniporous, or one to two multiporous, septula. Seen from the front the zooids are usually truncate distally and slightly attenuate proximally. Basal and lateral walls lightly calcified, the membrane occupying most of the front; orifice closed by a sphincter and no operculum can be distinguished. One or more spines may be present, usually confined to the distal angles of the zooid. In most species, a pedunculate avicularium shaped like a bird's head present on the side of all or many zooids. Ovicell hyperstomial, with calcified endooecium and membranous ectooecium; typically globular, but sometimes reduced to a hemisphere or less, closed by the inner vesicle which sometimes forms the major part of the ovicell.

In biserial species the arrangement of zooids at a bifurcation usually conforms to one of three patterns, originally described by Harmer (1923) as types 3, 4 and 5. The bifurcations are best studied from the basal side in stained and cleared preparations, but can generally be observed in a piece of a clean specimen viewed by transmitted light. The pattern of consecutive bifurcations is laterally reversed, so that the bifurcations immediately above and below any given one are mirror images of it. For descriptive purposes the zooids involved in the bifurcation are distinguished by letters (Fig. 4). The first zooid from which two

zooids are budded is referred to as A, the one beside it (which also buds two) as B. The outer zooids above A and B are C and D respectively while the inner zooids are E and F. In bifurcations of type 3 the axil is formed by zooids E and F. In type 4 the axil is formed by F and G (G being immediately distal to E in the same series). Zooid E is thus excluded from the axil, and the proximal part of G connects with F. In type 5 the enclosing process has been further extended so that both E and F are completely surrounded, and the axil is formed by G and H (Fig. 4). It should be noted, however, that the connecting portion between G and H may be very slender. In a further development of the enclosing process, several zooids may be surrounded; the branch then becomes quadriserial below the bifurcations.

Type species: *Sertularia neritina* Linnaeus, 1758.

Bugula dentata (Lamouroux)
(Fig. 4)

Acamarchis dentata Lamouroux, 1816: 135, pl. 3, figs 3a,b.

Bugula dentata: Busk, 1852b: 46, pl. 35, figs 1-5; Harmer, 1926: 439 (cum syn.), pl. 30, figs, 5,6; pl. 32, figs 21-25; Ryland 1974: 343; 1984: 68, fig. 4; Winston, 1986: 6.

Bugula sp.: Doak, 1971, colour plate 31 and rear cover; Coleman, 1977: 80 (colour plate).

DESCRIPTION

Colony tufted, not on a stalk, with some tendency to spiralling of branches; to 10cm. Branches narrow, of uniform width, the zooids biserial. Bifurcations of type 5, i.e., with two zooids wholly enclosed, most obvious in basal view. Zooids 0.6×0.25mm (basal), in Heron Island material. Opesia occupying three-fifths or more of the frontal surface; the external margin of the zooid inrolling proximally, narrowing the opesia. Inner distal angle with one spine, outer with two, sometimes long, and jointed at the base; a third outer spine some way below the other two. The spines of equal size on both sides of the branch, or the outer ones (with reference to the proximal bifurcation) much larger. Avicularia of two kinds: ordinary marginal avicularia attached about two-thirds way down the zooid, a little above or just below the vortex of the opesia; giant avicularia present or not. Ordinary avicularia about 0.2mm in length, a little less than the width of the bearing zooid at the point of attachment; dorsal profile of rostrum straight, its tip abruptly hooked (rectangular). Giant avicularia, when present, most often replacing normal avicularia on the two outer zooids (C, D) at bifurcations; much longer than the width of the bearing zooid; its entire upper profile convex, the rostral tip sometimes with lateral cusps; the mandible clavate, with a weak terminal point (Harmer, 1926, pl. 32, figs 21,23, 25). Ovicells globose, attached somewhat obliquely over the inner distal angle (Harmer, 1926,

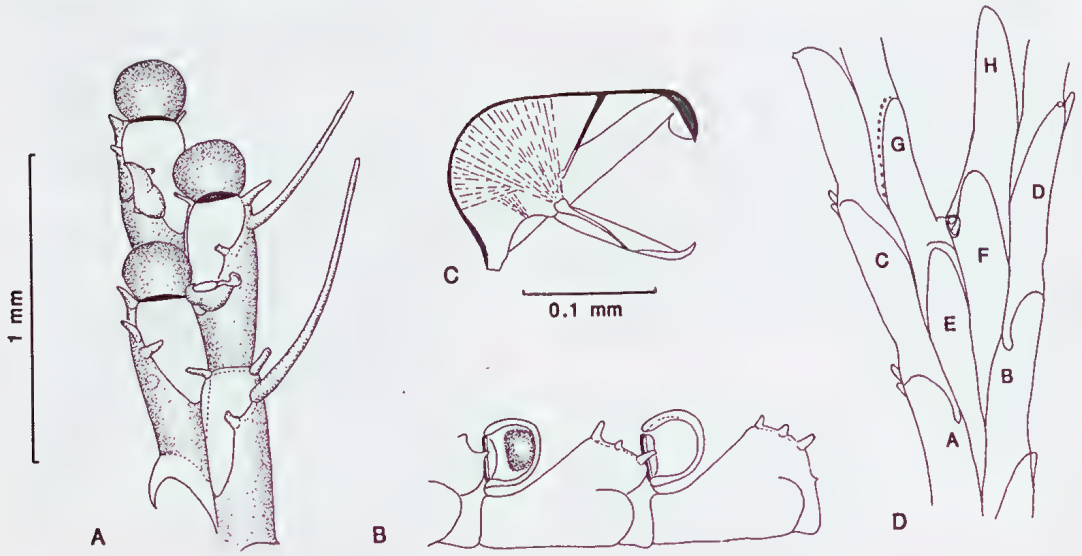


FIG. 4. *Bugula dentata*. A, Group of autozooids, with ovicells and avicularia. B, Autozooids in lateral view. C, Avicularium. D, Basal view of a dichotomy.

pl. 32, fig. 21) or wider than long, occupying the full width of the distal margin; surface calcification rippled; the closing membrane cuticularized.

REMARKS

The living colony is deep bottle green in colour, though acquiring a bluish sheen in flash photographs (Doak, 1971, pl. 31, & back cover; Coleman, 1977:80); on preservation the colour disappears leaving the colony of leaden appearance. The variability of this species was mentioned by Ryland (1974). In particular, the obliquely orientated ovicells, emphasized as diagnostic by Harmer (1926), seem to have been observed only in material from Indonesia. Giant avicularia have been recorded only from Singapore, the Banda Sea and Torres Strait. The normal, marginal avicularia are attached about two-thirds way down the outer wall of the zooid but, since the opesiae vary in length, the avicularian attachment may be either lateral or proximal relative to the opesia. The unusual and distinctively cuticularized ooecial closure, unremarked until 1974, characterizes all specimens from Madeira to New Zealand.

DISTRIBUTION

Widely distributed in the tropics and subtropics from Madeira and Cape Verde Is., to southern Africa, Indian Ocean (Amirante Island), Indonesia, Japan, Lifu, and northern New Zealand. In Australia, Coleman (1977) gives the depth range as 2-40 m; the habitat as rocky reefs, coral reefs and wharf piles; and its distribution to all States except N.T.

Bugula vectifera Harmer
(Fig. 5)

Bugula vectifera Harmer, 1926: 442, pl. 31, figs 1-6.

DESCRIPTION

Colony a loose spreading tuft, delicate, pale translucent straw-brown; to about 15mm in height; anchored proximally by rhizoids; the branches also attached to the substratum by intermittent rhizoids. Branches with zooids in two series, with type 4 bifurcations (Fig. 5D). Zooids weakly calcified; elongate, narrowed proximally, 0.55 (SD 0.03)×0.13 (SD 0.01)mm basally; opesia occupying about three-quarters of the frontal surface. No marginal spines. Avicularia attached on pedicels, proximal to the opesia,

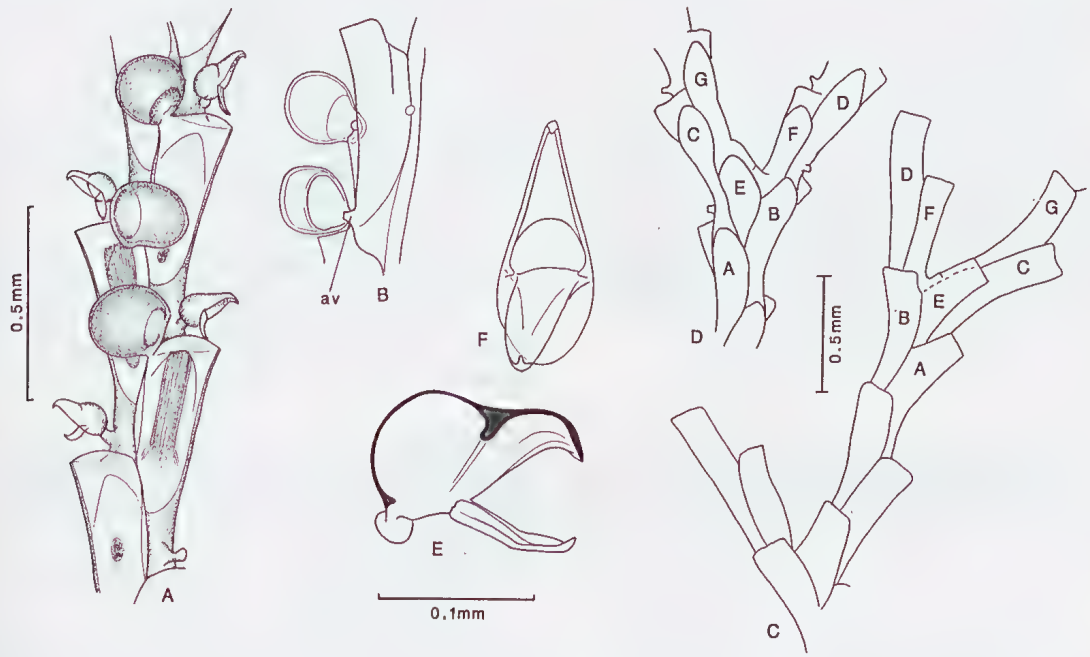


FIG. 5. *Bugula vectifera*. A, Group of autozooids, with ovicells and avicularia. B, Autozooids in lateral view, showing attachment of ovicells and avicularia. C, Part of a branch in basal view. D, A dichotomy in basal view. E, Avicularium. F, Palatal view of avicularium.

close to the distal margin of the preceding zooid; their length approximately equal to the terminal width of the preceding zooid; rostrum as long as the head, its tip sharply downcurved (Fig. 5E); width about the same as in *B. subglobosa* but, the rostrum being longer, lacking the swollen appearance of that species (Fig. 5F, cf. Fig. 6D). Ovicells prominent, a little longer than broad, narrowly attached to the inner distal angle of the bearing zooid (Fig. 5A,B), transversely orientated; the opening directed downwards and across the end of the bearing zooid, invisible from most viewpoints, close to the avicularium of the succeeding zooid. Embryos pale mahogany or pale purple-brown. Tentacle number 17-18, 'about 12' in Harmer's material.

DISCUSSION

Some differences are apparent between the Heron Island material and that described by Harmer. These probably relate mainly to the narrowness of the zooids in the Indonesian specimens (0.53 (SD 0.05) × 0.085 (SD 0.01)mm in British Museum specimen 1928.3.6.287, Borneo Bank), with 'their frontal surfaces sloping obliquely away from the median raised part of the branch'. In the Heron Island specimens this is slightly evident in the proximal part of the colony, but not elsewhere where the distal angles of the zooids tend to be raised well above the surface of the next distal zooid. Zooids tend to be uniserial proximally, though not to the extent described by Harmer in one of the Borneo Bank specimens; neither is there any longitudinal thickening here. Indeed, the habit of the colonies is semi-repent (*Scrupocellaria*-like) rather than arborescent, with a supporting stem. In other respects the agreement between the two groups of specimens is very close.

OCCURRENCE

Found, usually with *B. subglobosa*, among the under fauna of several boulders in the tract at Blue Pools, 27-31 Jul 1988. First record from Australia.

DISTRIBUTION

Great Barrier Reef, Java, Borneo Bank (Strait of Makassar), eastern Honshu, Japan (Harmer, 1926).

Bugula subglobosa Harmer
(Fig. 6)

Bugula subglobosa Harmer, 1926: 444, pl. 32, figs 15-18.

DESCRIPTION

Colony a loose spreading tuft, attached proximally by rhizoids, delicate, pale straw coloured, up to about 15mm; the branches also attached to the substratum by intermittent rhizoids. Branches with zooids in two series, with type 4 bifurcations (Fig. 6B). Zooids elongate, narrowing proximally, 0.59 (SD 0.04) × 0.13 (SD 0.01)mm basally; weakly calcified. Opesia occupying about three-quarters of the frontal surface. No marginal spines. Avicularia attached on pedicels, proximal to the opesia, almost under the distal edge of the preceding zooid; short (much shorter than the terminal width of the preceding zooid), very convex dorsally; the rostrum comprising less than half the total length, sharply downcurved (Fig. 6C); the head broad in relation to overall length, appearing swollen (hence *subglobosa*, Fig. 6D). Ovicells prominent, longer than broad, narrowly attached to the inner distal angle of the bearing zooid, transversely orientated (Fig. 6A); the opening directed downwards and across the end of the bearing zooid, concealed from most viewpoints, opposite the avicularium of the succeeding zooid. Embryos pale milky yellow. Tentacle number about 18.

The Siboga specimen (British Museum 1928.3.6.91) from North Celebes has larger zooids, 0.7 (SD 0.03) × 0.15 (SD 0.04)mm, but is of the same delicate colony form.

OCCURRENCE

Found, usually with *B. vectifera*, among the under fauna of several boulders in the tract at Blue Pools, 27-31 Jul 1988. First record from Australia.

DISTRIBUTION

Great Barrier Reef, Flores, Sumbawa, Timor, North Celebes and eastern Honshu, Japan (Harmer, 1926).

Family BEANIIDAE Canu & Bassler, 1927

Colony encrusting, loosely adherent, unilaminar; or erect, bilaminar, foliaceous; attached to substratum by rhizoids. Autozooids contiguous to widely disjunct, linked by long or short tubular extrusions of the mural septula.

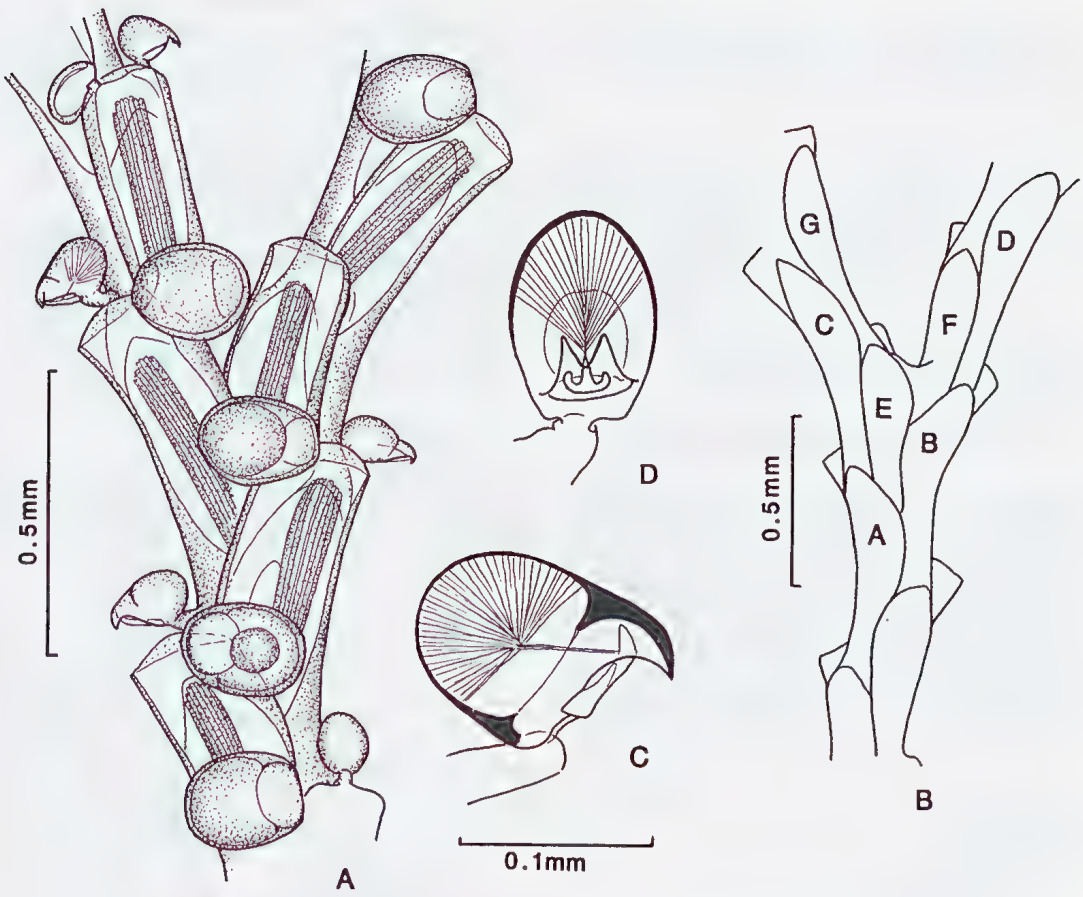


FIG. 6. *Bugula subglobosa*. A, Part of a branch, with autozooids bearing ovicells and avicularia. B, A dichotomy in basal view. C, Avicularium. D, Avicularium in distal view.

Frontal surface entirely membranous, with or without a border of marginal spines. Avicularia adventitious, pedunculate, of bird's head form. Ovicells present or absent.

Beania Johnston, 1840

Colony encrusting, unilaminar, ramifying or reticulate, attached to the substratum by rhizoids and generally loosely adherent. Autozooids closely packed, or widely spaced apart, but not contiguous, linked to each other by tubular extensions of mural pore chambers; recumbent, or erect, sometimes with an elongate, narrowly tubular, proximal portion. Frontal membrane occupying whole of broad distal portion of autozooid, bordered by thin spines in many species; distal spines or spinous processes present or absent. Avicularia present or absent; pedunculate, with a hooked rostrum. Ovicells reduced, vestigial or absent.

Type species: *Beania mirabilis* Johnston, 1840.

Beania magellanica (Busk)

Diachoris magellanica Busk, 1852b: 54, pl.67, figs 1-3.

Beania magellanica: Harmer, 1926: 412, pl. 28, figs 1-4, text- fig.1; Gordon, 1984: 46, pl. 11, fig. H.

DESCRIPTION

This species is distinguished from all other species of *Beania* by the six, regularly-arranged connecting tubes linking each autozooid with its neighbours, by a complete absence of spines, except for two to four tiny processes at the distal end of the autozooid, and by its greatly enlarged, paired avicularia. It is probably common in reef

habitats, but its filmy, transparent colonies are quite inconspicuous in the field, and only become readily apparent once specimens begin to dry.

DISTRIBUTION

Beania magellanica seems to be practically ubiquitous in tropical, subtropical and temperate seas. It has a circumpolar distribution in the Southern Ocean, though not extending into Antarctic waters, and in the western Pacific ranges northwards to Japan, and in the Atlantic region as far as the Mediterranean. It is certainly present in the eastern Pacific (Osburn, 1950) and probably occurs throughout the Indian Ocean.

Family CABEREIDAE Busk, 1852a

Colony erect, branching, jointed, attached to substratum by rhizoids; branches dividing dichotomously, unilaminar, with frontal and basal surfaces, autozooids in two, sometimes more, alternating longitudinal series. Autozooids well calcified, with moderately sized opesia; cryptocyst generally narrow, gymnocyst well developed. Spines present, or rarely, absent, one often modified as a flat plate, the scutum, overarching the frontal membrane. Avicularia adventitious, sessile, sometimes absent; vibracula generally present on basal surface. Ovicell hyperstomial, prominent.

Scrupocellaria van Beneden, 1845

Colony branching, erect and bushy, or repent and spreading; attached to the substratum by rhizoids. Branches biserial, with defined frontal and abfrontal faces, dividing dichotomously at regular intervals, each jointed at its base. Autozooids with well developed gymnocyst and oval frontal membrane; spines usually present at distal end of autozooid; a specially modified lateral spine, or scutum, present in many species, flattened and arching over the frontal membrane, sometimes hiding it completely. Heterozooids polymorphic: lateral avicularia typically present at outer distal angles of autozooids, often dimorphic; frontal avicularia often present on gymnocyst, also often dimorphic; vibracula typically present on abfrontal surfaces. Ovicell hyperstomial, globular, with or without pores, or larger fenestrae.

Type species: *Sertularia scruposa* Linnaeus, 1758.

Species of *Scrupocellaria* may be quite common in shallow reefal habitats, forming swards on the undersides of boulders, in association with other erect Cheilostomata, such as *Margaretta, Nellia* and *Vasignyella.* Three common tropical/subtropical species occur on the reef flats of Heron Island.

Scrupocellaria diadema Busk
(Fig. 7)

Scrupocellaria diadema Busk, 1852a: 370; 1852b: 24, pl. 28, figs 1-3.

Scrupocellaria diadema: Harmer, 1926: 375, pl. 25, figs 20-25; Ryland, 1984: 68, fig. 3; Hayward, 1988: 285, fig. 3C.

DESCRIPTION

This species forms stout, bushy, erect colonies. Autozooids 0.35–0.5mm long, with the opesia comprising about three-quarters total length; the

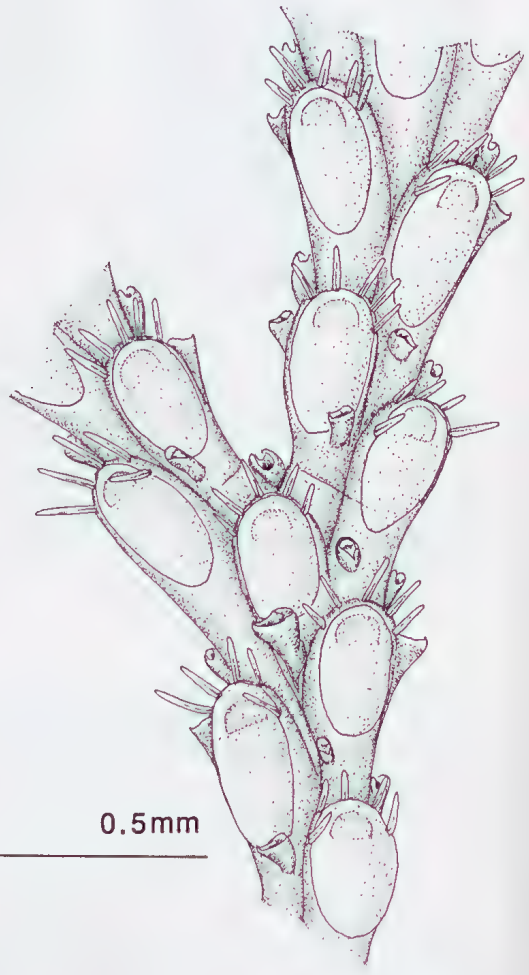


FIG. 7. *Scrupocellaria diadema.*

opesiae of the two series of autozooids overlapping along the branch. Each autozooid with two pairs of short, disto-lateral spines, and a single median distal spine; scutum narrowly oval, covering just the central area of the frontal membrane, but frequently absent. Disto-lateral avicularia small, monomorphic, a single, abfrontal vibraculum just visible distal to each; frontal avicularia shortly columnar, with the rostrum almost perpendicular to frontal plane, dimorphic, those borne by autozooids proximal to dichotomies greatly enlarged; a single vibraculum occurs in the axil of each dichotomy. Ovicell characteristic: wider than long, with conspicuous tubiform pores.

DISTRIBUTION

S. diadema was described from Moreton Bay, Queensland. It ranges northwards to Japan, throughout the Indo-Malaysian region, and westwards to India and Mauritius.

Scrupocellaria maderensis Busk
(Fig. 8)

Scrupocellaria maderensis Busk, 1860: 280; 1861: 77, pl. 32, fig. 1.
Scrupocellaria maderensis: Harmer, 1926: 372, pl. 25, figs 16-19; Gordon, 1984: 47, pl. 12, figs F,G; Ryland, 1984, fig. 2; Hayward, 1988: 283.

DESCRIPTION

Colony an erect, freely branching tuft, with the internodes between dichotomies often exceeding 2mm. Autozooids commonly about 0.35mm long; opesia small and round, comprising less than half total autozooid length, and those of the two autozooid series do not overlap along the branch. Up to four short spines on the outer distal corner of the autozooid, one or two on the inner; the scutum, invariably present, is rounded, with a straight distal edge, and almost completely hides the frontal membrane proximal to the operculum. Disto-lateral avicularia monomorphic, very large, with hooked rostrum, giving a serrated outline to the branch edge; frontal avicularia usually absent; vibraculum present on the abfrontal surface of each autozooid, and two in the axil of the dichotomy. Ovicell longer than wide, tilted towards axis of branch; flattened frontally, with a single fenestra.

DISTRIBUTION

Scrupocellaria maderensis is widely distributed in the warm temperate and tropical waters of the eastern Atlantic and Indo-West-Pacific regions. In the western Pacific it ranges from southern New Zealand to Japan.

Scrupocellaria spatulata (d'Orbigny)
(Fig. 9)

Cellularia spatulata d'Orbigny 1851: 50.
Scrupocellaria spatulata: Harmer, 1926: 382, pl. 26, figs 1-10; Winston & Heimberg, 1986: 7, figs 11-12; Hayward, 1988: 283.

DESCRIPTION

Colony forming delicate, spreading tufts up to 10mm high. Autozooids slender, 0.4-0.5mm long, the opesia comprising slightly less than half total frontal length; two series of opesiae just overlapping along the branch. Two or three spines on the outer distal corner of the autozooid, and usually two on the inner; non-ovicellate autozooids may have, in addition, one or two median distal spines; scutum narrowly oval, covering only a small central portion of the frontal membrane. Disto-lateral avicularia dimorphic: most usually tiny, with a laterally orientated, triangular mandible, occasionally

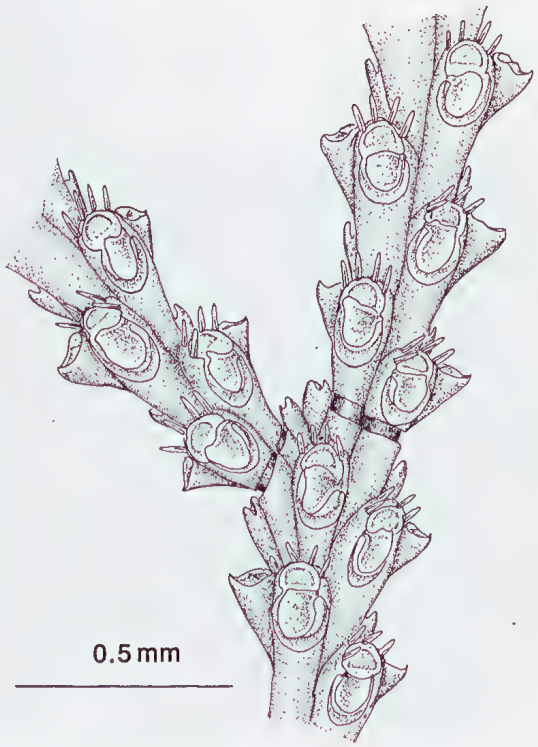


FIG. 8. *Scrupocellaria maderensis*.

FIG. 9. *Scrupocellaria spatulata.*

replaced by a grossly enlarged type with slender, digitate rostrum orientated parallel to the long axis of the branch; frontal avicularia sparse, monomorphic, columnar, situated close to the base of the scutum of the adjacent autozooid; a single vibraculum on the abfrontal surface of each autozooid, and one in the axil of each dichotomy. Ovicell as wide as long, globular, with small, regular perforations.

DISTRIBUTION

This species is distributed throughout the Indo-West-Pacific region, from Queensland to East Africa, and from Victoria northwards to the Philippines.

Superfamily MICROPOROIDEA Gray, 1848
Family MICROPORIDAE Gray, 1848

Colony encrusting or erect. Autozooids with membranous frontal wall underlain by an extensive cryptocyst; opesia reduced, often scarcely exceeding area of operculum; gymnocyst usually little developed. Spines present or absent. Avicularia present, adventitious, interzooidal or vicarious. Ovicells present or absent. Vertical walls with basal pore chambers or mural septula.

Micropora Gray, 1848

Colony encrusting. Autozooids typically flat, with lateral walls raised and thickened, and often developed as prominent umbones lateral to the opesia; frontal membrane entirely underlain by a thickly calcified, perforate cryptocyst, with paired opesiules situated close to its distal corners; opesia small, exactly coincident with orifice, with a thickened rim; no gymnocyst. Spines present or absent. Avicularia vicarious, smaller than autozooids; lacking in some species. Ovicells partly immersed, prominent, with small, scattered pores; closed by autozooid operculum. Vertical walls with large mural septula, which may extend to the basal wall.

Type species: *Flustra coriacea* Johnston, 1847.

Micropora angusta MacGillivray
(Fig. 10a)

Micropora coriacea var. *angusta* MacGillivray, 1887: 67.

Micropora sagittata d'Hondt, 1986: 712, pl. 6, figs 1,2.

DESCRIPTION

Colony loosely encrusting, forming flat, multilaminar sheets. Autozooids narrowly rectangular, 0.6-0.75 × 0.25-0.3mm; cryptocyst flat, finely granular, densely perforated, bounded by a thick, crenulate mural rim. Opesia raised above plane of cryptocyst, its lower lip almost perpendicular, thick, with a crenulate rim; more or less semicircular, with rounded corners. No oral spines. Opesiules indistinct. Avicularia relatively large; rostrum 0.16mm long, with broadly triangular mandible, proximo-laterally directed. Ovicell elongate oval, surface coarsely granular, with numerous tiny perforations; opesia of ovicellate autozooids longer than in non-ovicellate autozooids.

REMARKS

MacGillivray (1887) described the morphology of this species quite precisely although, regarding it simply as an interesting variant of *M. coriacea* Johnston, he unfortunately did not figure it or give a locality for his material. D'Hondt's material, which is unquestionably the same species as that from Heron Island, was from New Caledonia. P.L. Cook (in litt.) has re-examined MacGillivray's specimens of *M. coriacea* var. *angusta*, in the Victoria Museum, Melbourne, and reports that it is the same species as recorded here from Heron Island; specimen F45537A, Port

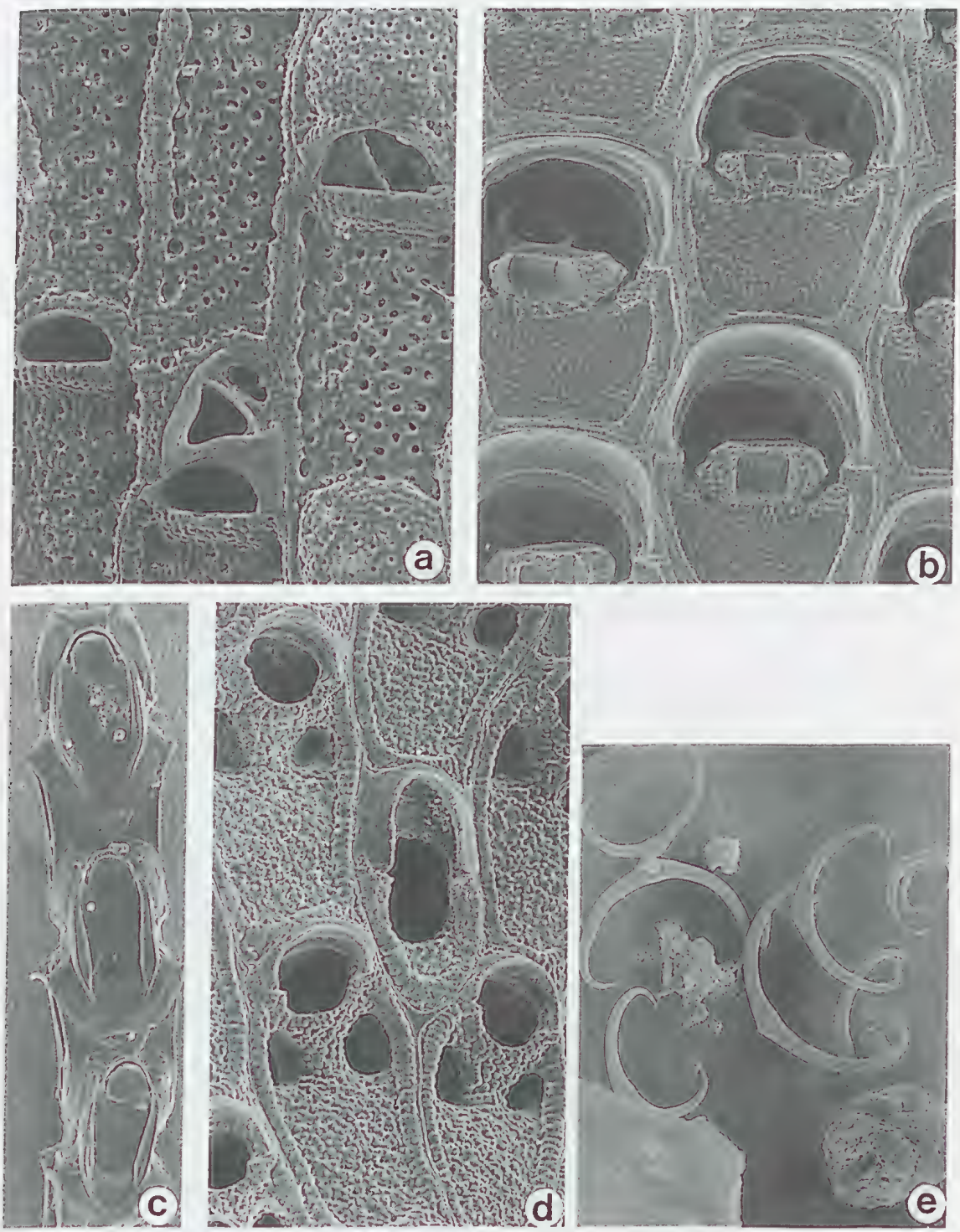


FIG. 10. a, *Micropora angusta*, ×110. b, *Steginoporella magnilabris*, ×50. c, *Nellia tenuis*, ×70. d,e *Thalamoporella stapifera*; d, autozooids and an avicularium, ×70; e, group of calipers, ×800.

Phillip Heads, is here designated as lectotype of *Micropora angusta* MacGillivray. The loosely encrusting, multilaminar colony form, and the finely punctate ovicell are unusual features for a species of *Micropora.*

Micropora variperforata Waters
(Fig. 2f)

Micropora variperforata Waters, 1887:51, pl.8, fig. 27.
Micropora variperforata: Gordon, 1986: 69, pl. 27, fig. B.

DESCRIPTION

Colony forming an irregular, spreading unilaminar sheet. Autozooids oval to hexagonal, 0.45-0.6×0.35-0.4mm; cryptocyst flat, nodular, with about 20-35 small, randomly distributed pores; opesiules recessed but distinct, proximolateral to opesia; an irregular series of comparatively large pores developed around the margins of the cryptocyst; mural rim crenulate, thickened, in later ontogeny continuous with a conspicuous proximal ridge of cryptocystal calcification. Opesia wider than long, 0.12-0.14 x 0.06-0.08mm; no oral spines. Avicularium scarcely larger than opesia; rostrum triangular, acute to frontal plane and laterally directed. Ovicell about as wide as long, the surface finely nodular, except for a smooth or faintly striated frontal band immediately above the aperture.

DISTRIBUTION

Several colonies occurred in sample 22, from the reef crest, northeast of the cay. The Heron Island specimens are strikingly similar to the Recent New Zealand material figured by Gordon (1986), so that *M. variperforata* is known from the western South Island of New Zealand as well as from New Zealand Tertiary deposits.

Family STEGINOPORELLIDAE Hincks, 1884

Colony encrusting; or erect, frondose or vinculariiform, attached by an encrusting base. Autozooids with well developed cryptocyst, which descends to basal wall in distal half of zooid, delimiting a tube for the exsertion of the polypide; gymnocyst reduced or lacking. Autozooids often dimorphic: unmodified *A* zooids represent majority; *B* zooids, perhaps primitive avicularia, are characterized by enlarged, toothed opercula. No ovicells. Vertical walls with multiporous mural septula.

Steginoporella Smitt 1873

Colony encrusting, or erect, frondose or narrow and branched. Autozooids typically dimorphic, both types containing polypides, distinguished principally by relative size of operculum. Frontal wall membranous, lacking a gymnocyst; underlain by a concave cryptocyst, which descends to the distal wall or to the basal wall in the distal half of the zooid, thus dividing its cavity into two chambers; withdrawn polypide located in proximal chamber, exserting via a tubular foramen ('polypide tube') in the distal part of the cryptocyst. Vertical walls of autozooids with large multiporous septula. No ovicells; embryos brooded within maternal autozooids. No spines. *B* zooids, characterized by enlarged and thickly sclerotized opercula, perhaps represent primitive vicarious avicularia.

Type species: *Membranipora magnilabris* Busk, 1854.

Steginoporella magnilabris (Busk)
(Fig. 10b)

Membranipora magnilabris Busk, 1854: 62, pl. 65, fig. 4.
Steganoporella magnilabris: Harmer, 1926: 277, pl. 17, figs 1-3, 7, 9, 12, text-fig. 10; Cook, 1964a: 53, pl. 1, fig. 4, text-fig. 2.
Steginoporella magnilabris: Winston, 1984: 10, figs 17,18.

DESCRIPTION

Colony forming extensive, flat, encrusting sheets, or occasionally erect, bilaminar or unilaminar plates; deep reddish-brown or horn-coloured. Autozooids rounded distally, straight proximally, commonly 0.9-1.0×0.6-0.7mm. Frontal membrane thick, opaque, bordered by a raised, crenulate mural rim; *A* zooids with distinctive semicircular operculum, as wide as zooid and about half as long, with a dark brown arched sclerite, and a submarginal series of small teeth on its inner face; *B* zooids, having proportionately much larger operculum, armed with stout, conspicuous, marginal teeth on its inner face, varying in frequency, from 0.2-30% in different geographical populations (Cook, 1964a). Cryptocyst occupying about half total length of autozooid, depressed, finely nodular, with numerous fine perforations; descending abruptly to basal wall of autozooid, with rounded polypide tube situated centrally in vertical distal part of cryptocyst and not visible in frontal view. Upper

distal edge of cryptocyst produced as a concave, or deeply cupped, process immediately above polypide tube. Distal half of autozooid with a raised rim supporting the operculum, below which is a broad oral shelf.

DISTRIBUTION

S. magnilabris occurs in shallow tropical waters, from the Caribbean, West Africa, East Africa and the Indian Ocean, Malaysia, Indonesia and the Philippines, and northwards to southern Japan.

Family THALAMOPORELLIDAE Levinsen, 1909

Colony encrusting or erect. Autozooids with frontal membrane entirely underlain by a granular, concave cryptocyst; opesia usually coincident with operculum; single or paired opesiules present, large. No gymnocyst. Avicularia vicarious. Ovicell large, bivalved; or lacking. Vertical walls with multiporous mural septula.

Thalamoporella Hincks, 1887

Colony encrusting or erect. Autozooids with membranous frontal wall underlain by extensive cryptocyst; no gymnocystal calcification. Cryptocyst concave or depressed, with a pair of large opesiules bounded by basally deflected cryptocyst, which may extend to the basal wall; opesia small, usually almost coincident with operculum. No spines. Avicularia vicarious. Ovicell bulbous; bivalved, with a longitudinal median suture, borne by a modified maternal zooid. Vertical walls with multiporous septula. Calcareous spicules, of unknown significance, present in cavity of autozooid.

Type species: *Flustra rozieri* Audouin, 1826.

Thalamoporella granulata Levinsen (Fig. 11a,b)

Thalamoporella granulata Levinsen, 1909: 789 (part), pl. 6a, figs 1a-f.
Thalamoporella granulata: Harmer, 1926: 297.

DESCRIPTION

Colony forming a flat, encrusting sheet. Autozooids rectangular to polygonal, bounded by low, crenulate, mural rims; 0.6-0.7×0.3-0.4mm. Cryptocyst with finely beaded surface, flat or slightly convex proximally, concave distally; opesiules irregularly oval, of unequal size, bounded proximally and laterally by descending cryptocyst which reaches to the basal wall of the autozooid; opesia with semicircular distal rim, its proximal edge shallowly concave. Avicularium as long as autozooid; rostrum constituting half total length, narrowly spatulate, curved laterally to left or right, the autozooid embraced by the curve consequently with an asymmetrically placed opesia. Brooding zooid shorter than autozooid, with proportionately broader opesia; capped by a thin-walled, bivalved ovicell, with triangular aperture closed by a modified operculum. Spicules of two types: widely opened compasses, of two sizes, and small, closed calipers.

DISTRIBUTION

The type locality for this species is Torres Strait; Harmer (1926) redescribed the material on which Levinsen (1909) founded *T. granulata*, but the species does not seem to have been reported subsequently from elsewhere. It appears common at Heron Island; large colonies were present in three of the samples reported on here.

Thalamoporella stapifera Levinsen (Fig. 10d,e)

Thalamoporella granulata var. *stapifera* Levinsen, 1909: 188, pl. 6, figs 5a-e.
Thalamoporella stapifera: Harmer, 1926: 297, pl. 19, figs 17,20,25; Soule & Soule, 1970: 10, figs 4C-G; Winston & Heimberg, 1986: 8, figs 13-16.

DESCRIPTION

Colony forming a broad, flat, encrusting sheet. Autozooids elongate, rectangular to irregularly hexagonal, bounded by thick, crenulate mural rims; 0.6-0.8×0.25-0.5mm. Cryptocyst more or less flat, slightly concave proximal to opesia; opesiules irregularly oval, of equal or unequal size, cryptocyst descending to basal wall, to form complete tube; opesia with semicircular distal rim, its proximal edge deeply concave. Avicularium shorter than autozooid; rostrum constituting less than half total length, symmetrical, distally rounded. Brooding zooid shorter than autozooid, with proportionately broader opesia, and especially pronounced opesiular tubes; ovicell thin-walled, bulbous, with triangular aperture closed by a modified operculum. Spicules of two types: widely open compasses, and large, wishbone-shaped calipers.

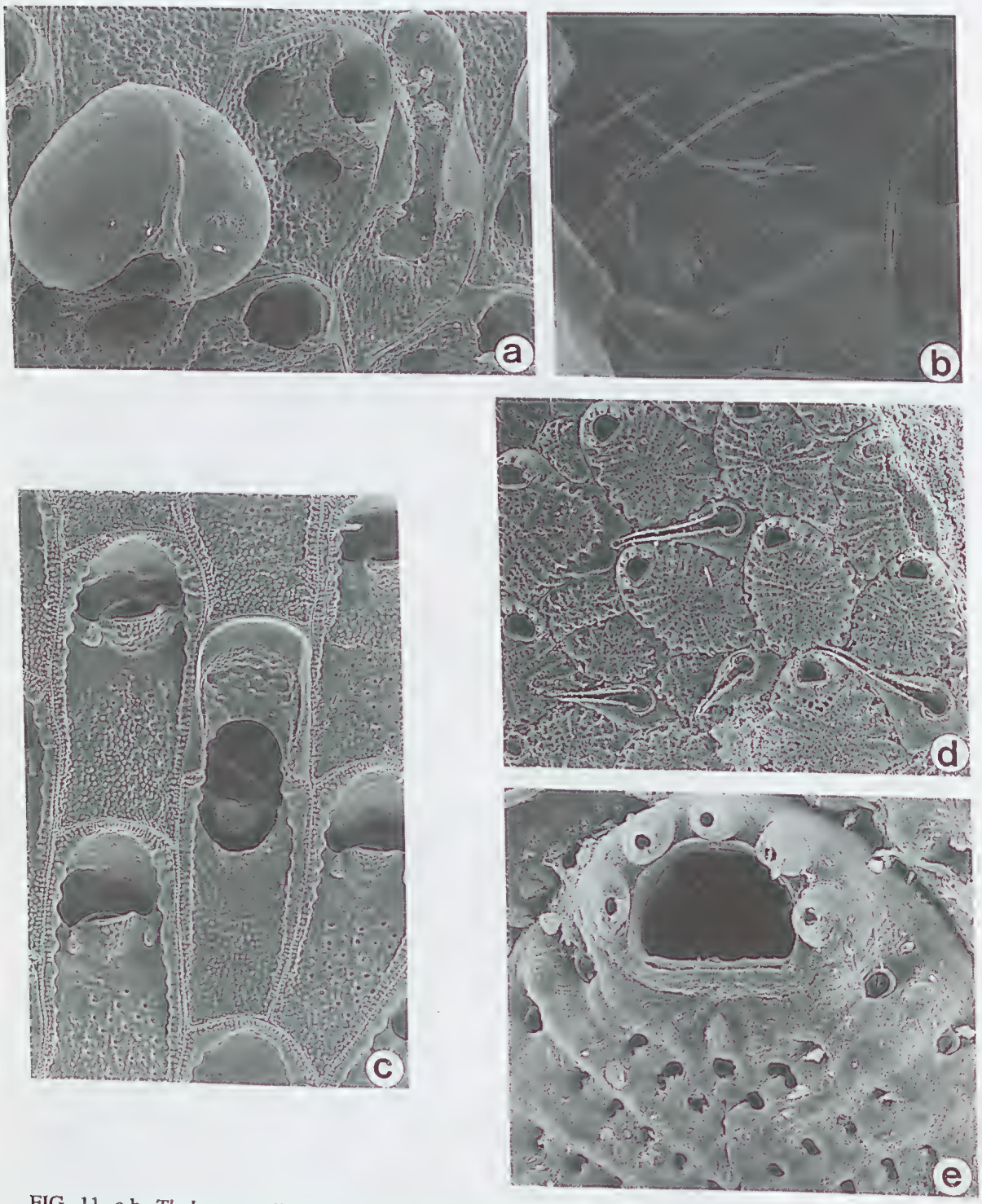


FIG. 11. a,b, *Thalamoporella granulata*; a, autozooids, an ovicell and an avicularium, ×70; b, group of compasses, ×250. c, *Labioporella bursaria*, ×60. d,e, *Puellina egretta*; d, ×65; e, ×400.

DISTRIBUTION

This species has been reported from Hawaii, Timor, Lombok and Mauritius, and is perhaps widely distributed through the Indo-West-Pacific realm. It has not been previously recorded from Australia. It was present in two of the Heron Island samples, numbers 24 and 26.

Labioporella Harmer, 1926

Colony encrusting or erect. Autozooids with membranous frontal wall underlain by extensive, porous cryptocyst; opesia constituting one-third or less of total length; no gymnocyst. Distal edge of cryptocyst deflected to meet basal wall, dividing cavity of cystid into two parts, forming a prominent tube through which the polypide passes on eversion. No spines. Avicularia vicarious, with extensive palatal cryptocyst; cystid divided by transverse septum, rostrum with proximo-lateral condyles but no crossbar. No ovicells. Vertical walls with multiporous septula.

Type species: *Labiopora crenulata* Levinsen, 1909.

Labioporella bursaria (MacGillivray) (Fig. 11c)

Amphiblestrum bursarium MacGillivray, 1887; 66, pl. 2, fig. 2.

Labioporella bursaria: Harmer, 1926: 285, pl. 21, figs 12, 15.

DESCRIPTION

Colony forming flat, unilaminar, encrusting sheets. Autozooids elongate, rectangular, separated by distinct sutures; 0.6-0.85×c. 0.35mm. Mural rim raised and crenulate in distal half of autozooid, smoothly rounded along middle portion of distal terminal wall for reception of operculum. Cryptocyst occupying three-quarters of autozooid length, finely granular, with a group of about 30 small pores in its middle region; flat, dipping sharply adjacent to polypide tube, which is markedly convex frontally, with a transversely oval aperture. Avicularia as large as autozooids; cryptocyst finely granular, imperforate, with an oval foramen through which a transverse, medially-thickened septum is visible, dividing the cystid cavity in half; rostrum slightly less than half length of avicularium, smoothly rounded, semi-elliptical, with thickened, proximo-lateral condyles.

DISTRIBUTION

Described by Harmer (1926) from Queensland and the Celebes, *L. bursaria* is also known from Victoria and South Australia. At Heron Island it occurred in two samples, from the reef flat and the reef crest south of the cay.

Suborder ASCOPHORINA Levinsen, 1909
Superfamily CRIBRILINOIDEA Hincks, 1879
Family CRIBRILINIDAE Hincks, 1879

Colony encrusting, sheet-like; or erect, attached by an encrusting base. Frontal surface of autozooids consisting of a shield of fused, flattened spines (costae) overarching the frontal membrane; costae hollow, often with one or more uncalcified spots (pelmatidia) and with intercostal spaces between the points of fusion permitting the passage of water to the space between the shield and the membrane. Distal oral spines present or absent. Avicularia adventitious or vicarious, or lacking. Ovicell hyperstomial. Vertical walls with basal pore chambers or mural septula.

Puellina Jullien, 1886

Colony encrusting, unilaminar. Autozooids with reduced proximal gymnocyst, and costate frontal shield covering whole of frontal membrane. Frontal shield consisting of radiating series of costae, each fused at intervals along lateral margins, with small intercostal pores between points of fusion; each costa with one or more uncalcified frontal pores (pelmatidia). Operculum D-shaped, closely fitting a calcified secondary orifice, proximal edge of which (apertural bar) is formed by the first pair of costae. Short, slender spines present around distal and lateral borders of orifice. A pair of slender, non-calcified papillae present, proximo-lateral to orifice, each protruding through a proximal intercostal pore. Avicularia interzooidal, with well-developed gymnocystal cystid. Ovicell hyperstomial, imperforate, closed by autozooid operculum. Basal pore chambers present. Ancestrula tatiform.

Type species: *Lepralia gattyae* Landsborough, 1852.

Species of *Puellina* are frequently characterized by the small size of both autozooids and colony. They are abundant in all temperate and tropical seas, apparently favouring biogenic carbonate substrata. They are all confusingly similar and many more species may exist than has been

previously recognized. Bishop & Household (1987) reviewed species of *Puellina* in British coastal waters, and redescribed and figured *P. innominata* (Couch), which, together with *P. radiata* (Moll), has been reported from almost all the world's seas. All records of these, and other, species of *Puellina* (formerly *Cribrilaria*) need to be examined in the light of Bishop & Household's (1987) work. The three species here described from Heron Island have probably been reported previously from Queensland and adjacent areas as *P. innominata* or *P. radiata*. Features important in identifying species of *Puellina* are: size and shape of orifice, number of spines, form of the suborificial lacuna, and morphology of the avicularium.

Puellina decipiens sp. nov.
(Fig. 12d,e)

TYPE MATERIAL
HOLOTYPE: GH5225, Heron Island, Stn 22, 15 Apr 1972.

ETYMOLOGY
Latin *decipio, -ere*, to beguile or cheat.

DESCRIPTION
Autozooids broadly oval, flat, separated by shallow grooves. Gymnocyst limited to a narrow, proximal band; frontal shield consisting of about 16 fused costae, each with a pronounced tubercle basally (i.e., at periphery) bearing the single pelmatidium. A single, large, transversely oval lacuna immediately proximal to the apertural bar. Secondary orifice wider than long, with five, evenly spaced disto-lateral spines, four persisting in ovicelled autozooids. Avicularia infrequent; cystid small, inconspicuous, rostrum elongate triangular. Ovicell slightly wider than long, with indistinct longitudinal carina.

Measurements (means and standard deviations of 20 values, mm): autozooid length 0.29±0.02; width 0.21±0.02; orifice length 0.05±0.002; width 0.06±0.003; avicularium length 0.10± 0.01 (n = 14).

REMARKS
The short avicularium is very similar to that of the European *P. innominata* (Couch), but *P. decipiens* differs from that, and other, species of *Puellina* in its very large subapertural lacuna and flat, non-umbonate frontal shield.

Puellina egretta sp. nov.
(Fig. 11d,e)

Cribrilaria aff. *radiata*: Ristedt, 1985: 20, fig. 3e-h .

TYPE MATERIAL
HOLOTYPE: GH5226, Heron Island, Stn 12, 12 Apr 1972.

ETYMOLOGY
French *aigrette*, a heron.

DESCRIPTION
Autozooids broadly oval to irregular, flat, separated by deep grooves. Gymnocyst minimally developed, inconspicuous; frontal shield formed from about 19 fused costae, each broadened but scarcely tuberculate proximally, pelmatidia indistinct. Apertural bar with a small median thickening, proximal to which is a small, round lacuna, clearly distinct from the first series of intercostal pores. Secondary orifice wider than long; five closely spaced oral spines present. Avicularia frequent; cystid well developed, with broad, smooth gymnocyst; rostrum slender, elongate, directed disto-medially along the border of the adjoining autozooid. Ovicell not found.

Measurements (means and standard deviations of 20 values, mm): autozooid length 0.34±0.03; width 0.27±0.03; orifice length 0.05±0.003; width 0.07±0.005; avicularium rostrum length 0.24±0.05.

REMARKS
This species develops rather larger colonies than the other two described here, and is thus more immediately obvious. The broad, flat autozooids and numerous elongate avicularia are especially distinctive.

DISTRIBUTION
Ristedt (1985) figured specimens of a *Puellina* from the Seychelles and the Philippine Islands which are clearly referable to *P. egretta*.

Puellina vulgaris sp. nov.
(Fig. 12b,c)

TYPE MATERIAL
HOLOTYPE: GH5227, Heron Island, Stn 23, 16 Apr 1972.

ETYMOLOGY
Latin *vulgaris*, commonplace or ordinary.

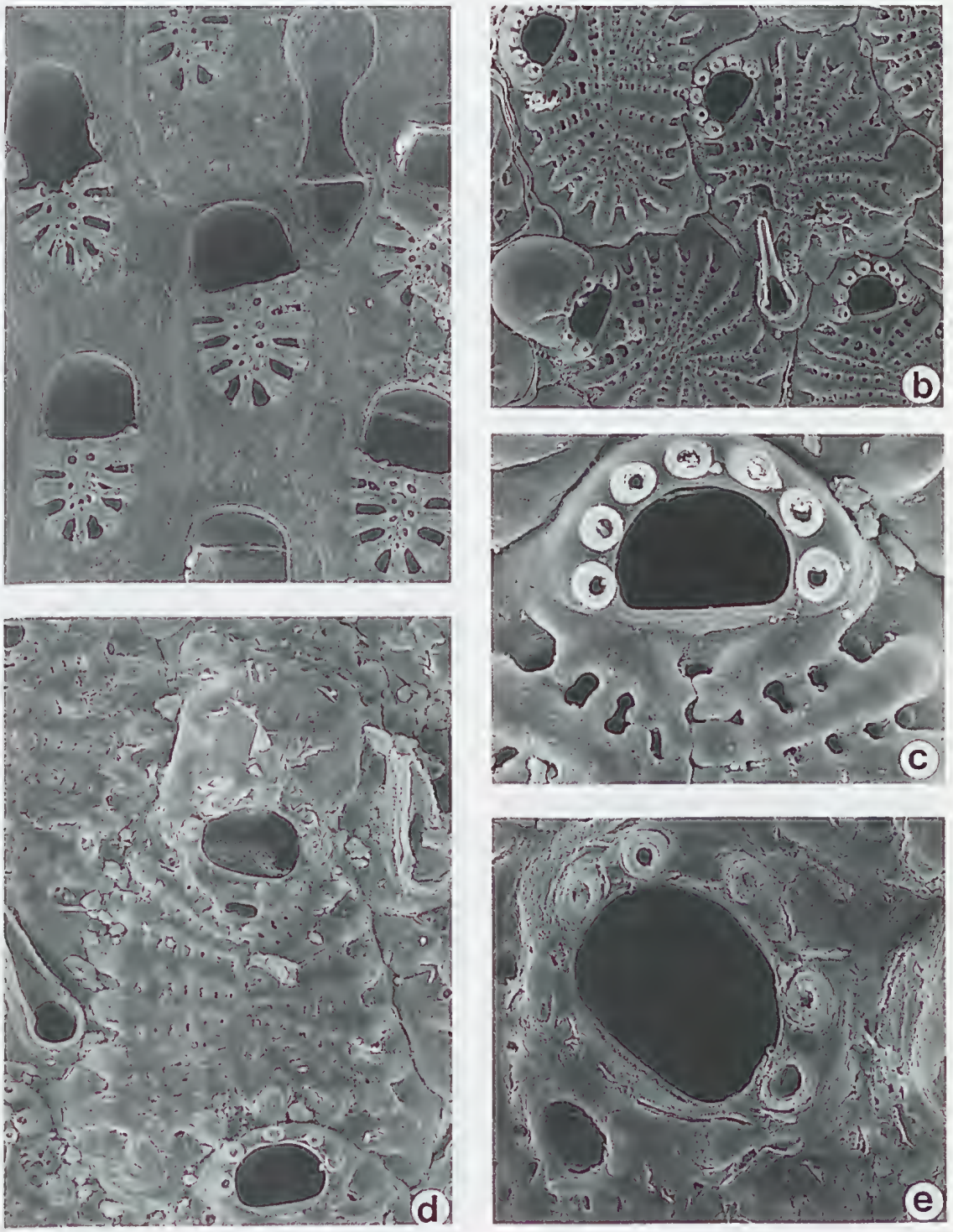


FIG. 12. a, *Figularia fissa*, ×75. b,c, *Puellina vulgaris*; b, ×130; c, ×450. d,e, *Puellina decipiens*; d, ×220; e, ×500.

DESCRIPTION

Colony forming small unilaminar patches. Autozooids oval, convex, separated by deep grooves. Gymnocyst clearly visible as a smooth border around the autozooid; frontal shield formed from 15-16 costae, each broadened proximally but not tuberculate; pelmatidia indistinct; intercostal pores relatively large, particularly in distal half of shield. A single, moderately sized subapertural lacuna present. Secondary orifice wider than long, with seven closely spaced spines, four persisting in ovicelled autozooids. Avicularia infrequent; cystid small, indistinct; rostrum narrowly triangular, relatively short, directed distally or disto-laterally. Ovicell spherical, as wide as long, with a small frontal umbo. Measurements (means and standard deviation of 20 values, mm): autozooid length 0.27±0.02; width 0.21±0.02; orifice length 0.04±0.003; width 0.05±0.005; avicularium rostrum length 0.12±0.02 (n = 5).

REMARKS

The seven oral spines, conspicuous subapertural lacuna, and rather small avicularium together distinguish this species from other tropical species of *Puellina.*

Figularia Jullien,1886

Colony encrusting. Autozooids with well-developed gymnocyst and, often extensive, costate frontal shield; costae fused medially and along their length, with a few irregular pores between the points of fusion, and with one or more pseudopores on each. Aperture rounded-quadrangular; operculum pivoting on lateral condyles, frequently compound, with a transverse line of flexure level with the condyles. Oral spines present or absent. Avicularia vicarious or interzooidal, generally sparse. Ovicell hyperstomial, prominent, closed by autozooidal operculum; typically with a longitudinal, median suture, and one or more large pores, or fenestrae, on each side. Vertical walls with uniporous or multiporous septula. Ancestrula tatiform.

Type species: *Lepralia figularis* Johnston, 1847.

Figularia fissa (Hincks) (Fig. 12a)

Cribrilina figularis var. *fissa* Hincks, 1880a: 196, pl. 26, fig. 8.

Figularia fissa: Harmer, 1926: 478, pl. 34, figs 19-23.

DESCRIPTION

Colony forming extensive, unilaminar sheets; brownish-coloured, with the opercula of the autozooids conspicuously dark mahogany. Autozooids elongate, convex, with costate frontal shield comprising about one-third total length; 0.55-0.8 × c.0.35mm. Costae flat, 8-10 in total; widely spaced, with elongate gaps between, each with a single, distal, pseudopore. Avicularia rare, about as long as autozooid, with a striking, spoon-shaped rostrum. Ovicell wider than long, the ectooecium on each side of the median suture with an elongate, curved, frontal fenestra.

REMARKS

This distinctive species is immediately recognized by its costate frontal shield, which has relatively few, widely spaced costae, and by its characteristic avicularia. *F. fissa* is evidently quite common at Heron Island, and was present in four of the samples described here.

DISTRIBUTION

F. fissa does not seem to have been recorded previously from Australia; it is known to occur in the Indo-Malayan region, from Singapore to New Guinea, and perhaps has a limited distribution in the western Pacific.

Superfamily CATENICELLOIDEA Busk, 1852a
Family SAVIGNYELLIDAE Levinsen, 1909

Colony erect, consisting of branching, uniserial chains of autozooids; jointed, each internode formed from a single clavate autozooid. Frontal wall of autozooids a porous gymnocyst, with or without mural septula; orifice with or without a sinus, its proximal rim sometimes formed from a pair of fused costae; oral spines present or absent. Avicularia adventitious, adjacent to orifice, or lacking. Ovicell present or absent.

Vasignyella Gordon, 1989a

Colony erect to repent, attached by rhizoids. Autozooids elongate, clavate, in branching uniserial chains. Frontal wall largely gymnocystal, with scattered pores; proximal side of orifice bordered by a pair of small, fused costae. No spines. Avicularia paired, lateral to orifice. Ovicell unknown. Large uniporous septula in lateral walls of autozooid.

Type species: *Catenaria otophora* Kirkpatrick, 1890b.

Vasignyella otophora (Kirkpatrick) (Fig. 14a)

Catenaria otophora Kirkpatrick, 1890b: 17, pl. 5, figs 1a-c.
Savignyella otophora: Harmer, 1957: 763, pl. 51, figs 19-21.
Vasignyella otophora: Gordon, 1989a: 453, figs 13-15.

DESCRIPTION

Colony erect or repent, attached to the substratum by delicate, chitinous rhizoids; composed of uniserial chains of slender, clavate autozooids, branching at irregular intervals. Autozooids very lightly calcified, clavate or fusiform, broadest distally, tapered proximally; 1.0-1.3×0.25mm. Primary orifice terminal, about as wide as long, the proximal edge shallowly concave between indistinct condyles; proximal border of orifice formed by a pair of short, fused costae. Frontal wall evenly perforated by large, round pores; a row of about five large, uniporous septula in each lateral wall. Avicularia lateral to orifice, paired; the rostrum triangular, distally directed, projecting conspicuously. Each autozooid buds another from its disto-basal surface, and one or more additional autozooids may be budded from the lateral septula; the proximal part of each autozooid, immediately above its point of origin, is uncalcified, and appears as a brown, cuticular node.

DISTRIBUTION

V. otophora is probably widely distributed throughout the Indo-West-Pacific realm, but is particularly inconspicuous and has been reported on very few occasions. Most records are centred on the Indo-Malayan region, but it has also been recorded as far west as the Sudanese Red Sea (Dumont, 1981) and, to the east, from Samoa (Gordon, 1989a).

Superfamily HIPPOTHOOIDEA Busk, 1859
Family HIPPOTHOIDAE Busk, 1859

Colony encrusting or erect. Various zooid polymorphs occur, including female zooids and dwarf zooeciules. Autozooids with gymnocystal frontal wall; imperforate, or with small punctae and/or tubercles. Primary orifice rounded or sinuate; condyles present; oral spines generally lacking. Avicularia interzooidal or vicarious, or absent. Ovicell hyperstomial, closed by zooidal operculum; or absent. Vertical walls with basal pore chambers and small mural septula.

Hippothoa Lamouroux, 1821

Colony encrusting, consisting of branching, uniserial chains of polymorphic zooids. Autozooids clavate, with a slender, stolon- like proximal portion; ovicellate female zooids often smaller than autozooids, ovicell with frontal umbo or apical perforation, closed by zooidal operculum; zooeciules minute, cylindrical, with simple orifice, of unknown function. Frontal wall imperforate, smooth, or ridged. Primary orifice with sinus and distinct condyles; no oral spines. No avicularia. Tubular pore chambers in lateral walls. Ancestrula kenozooidal or tatiform.

Type species: *Hippothoa divaricata* Lamouroux, 1821.

Hippothoa calciophilia Gordon (Fig. 13a,b)

Hippothoa calciophilia Gordon, 1984: 108, text-fig. 10; pl. 42, figs A-C.

DESCRIPTION

Colony diffuse, spreading widely over the substratum; zooid chains branching in a cruciform manner, each zooid producing one distal and paired lateral buds. Distal, clavate portion of autozooid about 0.3×0.15mm; filiform proximal portion 0.02mm wide, 1-1.5×length of distal portion. Primary orifice slightly longer than wide, commonly 0.06×0.05mm, with a deep, broad, U-shaped sinus, and small, rounded condyles. Frontal wall steeply convex, often with fine, transverse corrugations, and a longitudinal ridge. Female zooids most usually laterally budded from autozooids, the distal portion of similar size to autozooids, the filiform proximal portion usually shorter; ovicell with semicircular aperture, and a single, small, apical perforation. Zooeciules sporadic, budded from either or both of the two basal pore chambers on each side of an autozooid; 0.05-0.1mm long, with minute distal orifice.

REMARKS

H. calciophilia has only recently been distinguished from other species of *Hippothoa* (Gordon, 1984). It is probably widely distributed throughout the Great Barrier Reef province, but its small size and cryptic habits render it very inconspicuous.

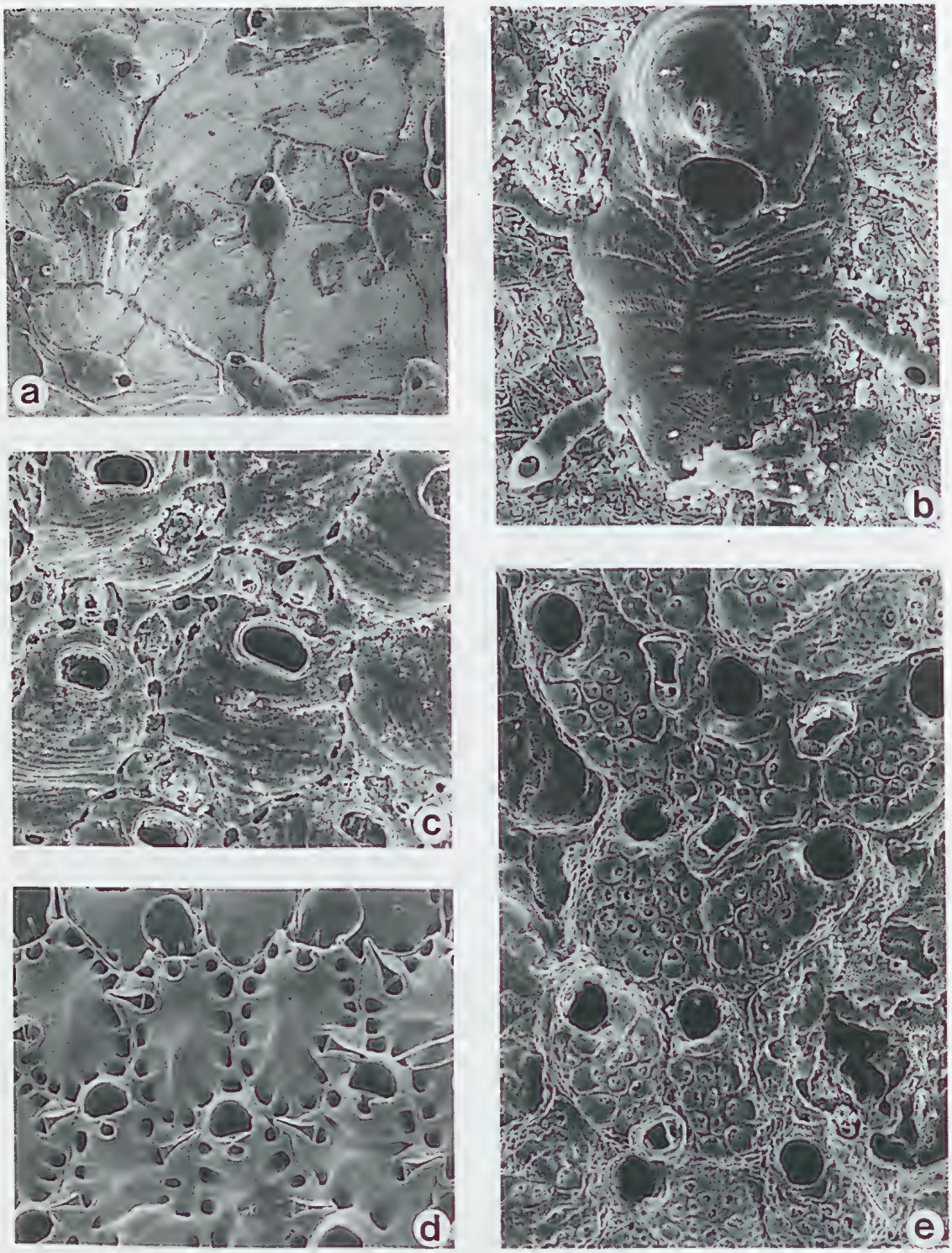


FIG. 13. a,b, *Hippothoa calciophilia*; a, part of a colony, ×50; b, a female zooid, with zooeciules, ×215. c, *Chorizopora brongniartii*, ×85. d, *Exochella conjuncta*, ×70. e, *Tremogasterina spathulata*, ×65.

Family CHORIZOPORIDAE Vigneaux, 1949

Colony encrusting, unilaminar. Frontal wall of autozooids imperforate, or with minute punctae. Primary orifice semicircular, without a sinus. Avicularia interzooidal. Ovicell hyperstomial, imperforate. Small kenozooids present. Vertical walls with tubular basal pore chambers.

Chorizopora Hincks, 1879

Colony encrusting, forming thin unilaminar sheets. Autozooids slightly disjunct, linked by tubular extensions of the basal pore chambers. Frontal wall gymnocystal, thinly calcified, imperforate. Primary orifice semicircular or D-shaped; oral spines present or absent. Avicularia vicarious, smaller than autozooids; small kenozooids with rounded membranous frontal fenestrae interspersed among autozooids. Ovicell hyperstomial, imperforate, closed by autozooid operculum.

Type species: *Flustra brongniartii* Audouin, 1826.

Chorizopora brongniartii (Audouin)
(Fig. 13c)

Flustra brongniartii Audouin, 1826: 240; Savigny pl. 10, fig. 6.
Chorizopora brongniartii: Hayward & Ryland, 1979: 240, fig. 103; Gordon, 1984: 113, pl. 44, fig. C; Hayward, 1988: 327.

REMARKS

The thin, hyaline colonies of *C. brongniartii* are inconspicuous on the carbonate substrata it appears to favour and are easily overlooked in wet material. At least three other species of *Chorizopora* are known from New Zealand (Gordon, 1984), but *C. brongniartii* is readily recognized by the smooth or transversely wrinkled, but non-spinous, frontal walls of its autozooids.

DISTRIBUTION

C. brongniartii is widely distributed in all temperate and tropical shelf seas.

Superfamily ARACHNOPUSIOIDEA Jullien, 1888
Family EXECHONELLIDAE Harmer, 1957

Colony encrusting. Autozooids with perforated, umbonuloid frontal wall. Orifice with well marked peristome; lacking spines. Avicularia adventitious and/or vicarious or interzooidal. Ovicells present or absent.

Tremogasterina Canu, 1911

Colony encrusting or erect, multilaminar. Autozooids with umbonuloid frontal wall, perforated by few, large, frontal foramina, and with small marginal pores. Calcified orifice rim with lateral condyles; no oral spines. Avicularia interzooidal and/or vicarious. Ovicells prominent, hyperstomial, imperforate; not closed by autozooid operculum. Autozooids linked by large, multiporous septula. Ancestrula tatiform.

Type species: *Tremogasterina problematica* Canu, 1911.

Tremogasterina has a worldwide distribution, in shallow coastal waters, between the 30° north and south parallels. The genus was studied in detail by Cook (1977).

Tremogasterina spathulata (Canu & Bassler)
(Fig. 13e)

Hiantopora spathulata Canu & Bassler, 1929: 116, pl. 11, figs 13, 14.
Arachnopusia spathulata: Harmer, 1957: 657, pl. 68, figs 22, 23, 25, 31.
Tremogasterina spathulata: Cook, 1977: 136, pl. 5, fig. A; text- figs 1B, 5A.

DESCRIPTION

Colony forming small, unilaminar patches, generally inconspicuous. Autozooids oval, convex, separated by deep grooves; 0.5-0.6×0.3-0.4mm. Orifice longer than wide, narrowest proximally; proximal edge more or less straight, thickened, and frequently with a short, suboral mucro. Four or five delicate, distal spines present. Frontal wall with a variable number (2-20) of irregular foramina, each with a broad, thick rim, the sutures between giving a tessellated effect; marginal pores inconspicuous. Avicularia sporadic, developed on disto-lateral borders of autozooids, 0.2mm long, typically distally directed; rostrum spatulate, with straight distal edge, upcurved. Ovicell wider than long.

DISTRIBUTION

Widely distributed in the Indo-West-Pacific region, from the Red Sea to the Philippines. *T. spathulata* is essentially a shallow water species, and its small colonies occur on coral rubble and other hard substrata; on Mauritian reefs it is especially common on the inner reef flat (Hayward,

1988). At Heron Island it was present in half of the samples studied to date.

Superfamily UMBONULOIDEA Canu, 1904
Family EXOCHELLIDAE Bassler, 1935

Colony encrusting or erect. Autozooids with umbonuloid frontal shield bordered by conspicuous marginal pores. Orifice with well developed peristome, incorporating one or more denticles on its inner, proximal edge; oral spines present. Avicularia adventitious. Ovicell present. Vertical walls with basal pore chambers or mural septula.

Exochella Jullien,1888

Colony encrusting, unilaminar. Frontal wall of autozooids umbonuloid, imperforate other than for a single series of large, marginal pores. Orifice obscured in early ontogeny by a complex peristome, its lobed proximal edge corresponding with ridges on its inner face which delimit one or two narrow channels; at the lip of the peristome, these channels may close distally to form one or two distinct spiramina. Oral spines typically present. Avicularia adventitious, budded from marginal pores (frontal septula) proximo-lateral to orifice; one, two, or more per autozooid, usually with acuminate rostrum. Ovicell spherical, imperforate, sometimes partly immersed, not closed by autozooid operculum. Basal or mural pore chambers present.

Type species: *Mucronella tricuspis* Hincks, 1881c.

Exochella is distributed almost exclusively in the southern hemisphere. There are several Antarctic species, and a number of others from cold temperate or subantarctic waters of South America, the Southern Indian Ocean and New Zealand (Hayward, 1991). *E. conjuncta* Brown is the only species known to range into tropical waters.

Exochella conjuncta Brown
(Fig. 13d)

Exochella conjuncta Brown, 1952: 294, figs 220-223.
Exochella conjuncta: Gordon, 1989b:30, pl.14, fig. A.

DESCRIPTION

Colony forming small, rounded patches. Autozooids oval to hexagonal, convex, separated by thickened ridges which become indistinct in later ontogeny; small, 0.35-0.4 by about 0.25mm. Frontal wall with few, large, marginal pores; thickening steadily, becoming vitreous and smooth, with the boundaries of each autozooid marked only by the pronounced, rounded, marginal pores. Peristome with paired inner ridges, delimiting a single median channel, opening externally as an oval spiramen. Two short, distal, oral spines present in newly budded autozooids, obscured by development of peristome. One or two avicularia per autozooid, 0.13mm long, with slender, laterally-directed rostrum. Ovicell spherical, smooth, largely immersed and hidden in later ontogeny.

DISTRIBUTION

E. conjuncta was first described from Pliocene deposits of New Zealand (Brown, 1952), and subsequently shown to have a Recent distribution extending from the South Island of New Zealand to New South Wales (Gordon, 1989b). Its presence at Heron Island marks a considerable extension in its known range.

Family CELLEPORARIIDAE Harmer, 1957

Colony encrusting, multilaminar, massive or nodular; often erect, developing stout, irregular branched or lobed forms; or pisiform, encrusting erect substrata; or discoidal and unattached. Autozooids recumbent to erect, typically without regular orientation; frontal wall umbonuloid, with marginal pores. Orifice without a sinus, with or without one or more proximal denticles; oral spines present or absent. Avicularia adventitious, associated with orifice, and vicarious; typically polymorphic. Ovicells present.

Celleporaria Lamouroux, 1821

Colony encrusting, or erect and irregularly branched, or massive; multilaminar, developed by frontal budding of successive autozooid generations. Autozooids recumbent at growing margins, elsewhere suberect, with varying orientation. Frontal wall umbonuloid, with indistinct marginal pores. Oral spines typically present. Avicularia adventitious and vicarious, frequently polymorphic. Ovicell hyperstomial, small and spherical, imperforate.

Type species: *Cellepora cristata* Lamarck, 1816.

This genus is widely distributed in tropical and subtropical seas, with many species reported from shallow reef habitats. Colonies are often large, and conspicuously pigmented. Unfor-

tunately, identification is often difficult. The taxonomy of *Celleporaria* is confused, at least partly because many species have still to be named, and a majority of described species are poorly known and have never been adequately illustrated.

Celleporaria tridenticulata (Busk)
(Fig. 14b,c)

Cellepora tridenticulata Busk, 1881: 343,344,347, pl. 26, fig. 9; 1884: 198, pl. 29, fig. 3; pl. 35, fig. 17.
Celleporaria tridenticulata: Harmer, 1957: 670, pl. 42, figs 5-10; Gordon, 1984: 115, pl. 45, figs C-E.

DESCRIPTION

The aperture of *C. tridenticulata* bears three conspicuous denticles on its concave proximal border, which may be pointed, truncate, bifid, or even trifid. It has two (rarely three or four) slender, distal oral spines, and a median, proximal, suboral avicularium on a short umbonate cystid, with the oval rostrum acute to the orifice plane and facing laterally. Vicarious avicularia vary from 0.3 to 0.5mm long, with a slender rostrum, slightly spatulate distally, with a finely serrate edge, and a stout crossbar, which lacks a columella.

DISTRIBUTION

Described originally from Torres Strait, this species has been recorded from throughout the Great Barrier Reef province, from New South Wales, Victoria and New Zealand. It is distributed through the Indo-Malaysian Archipelago, westwards to India, Sri Lanka and Mauritius. Canu & Bassler's (1930) record from the Galapagos Islands should perhaps be re-examined.

REMARKS

C. vagans (q.v.) also bears three, thin, pointed denticles on the proximal border of the orifice. It is distinguished from *C. tridenticulata* by its lack of oral spines; by its deeply notched peristome; and by its vicarious avicularium, which is more slender than that of *C. tridenticulata*, with a smooth edge to the rostrum and a distinct columella.

Celleporaria aperta ((Hincks)
(Fig. 14d,e)

Schizoporella aperta Hincks, 1882: 126, pl. 5, fig. 3.
Celleporaria aperta: Harmer, 1957: 673 (in part); Winston & Heimberg, 1986: 32, figs 79-84.

DESCRIPTION

Colony multilaminar and nodular, but rather small, rarely occupying more than a few cm^2 of substratum. Recumbent autozooids commonly 0.5×0.3mm, with convex, nodular frontal wall; marginal pores few, small and indistinct. Primary orifice wider than long, about 0.1×0.15mm, the proximal border slightly concave, with a shallow, irregularly U-shaped sinus medially; condyles small, pointed, inconspicuous; typically with two, widely spaced, disto-lateral spines, and occasionally with a third, distally situated. Suboral avicularium characteristic: proximal to sinus, small, with oval rostrum, finely denticulate distally, 0.05mm long; perpendicular to plane of orifice and facing laterally. Vicarious avicularia sporadic, rostrum commonly 0.2-0.3mm long, parallel-sided, and rounded distally, or rather lanceolate with a tapered distal tip; crossbar stout, flattened. Ovicell shallow, imperforate, with finely nodular calcification.

REMARKS

Winston & Heimberg (1986) re-examined some of the material studied by Harmer (1957), and considered that he had confused several species of *Celleporaria* in his account of *C. aperta*.

DISTRIBUTION

C. aperta seems to be widely distributed in the western Pacific, from the South China Sea to Queensland, and throughout the East Indies, ranging to Sri Lanka and East Africa. Its reported occurrence from West Africa, Cape Verde Islands (Cook, 1968b, 1985) and the Caribbean should be regarded with caution until specimens from those regions have been examined by SEM.

Celleporaria desperabilis sp. nov.
(Fig. 15e,f)

TYPE MATERIAL

HOLOTYPE: GH5228, Heron Island, Stn 14, 12 Apr 1972.
PARATYPE: GH5229, as for holotype.

ETYMOLOGY

Latin *despero, desperabilis*, hopeless.

DESCRIPTION

Colony forming a multilaminar, encrusting

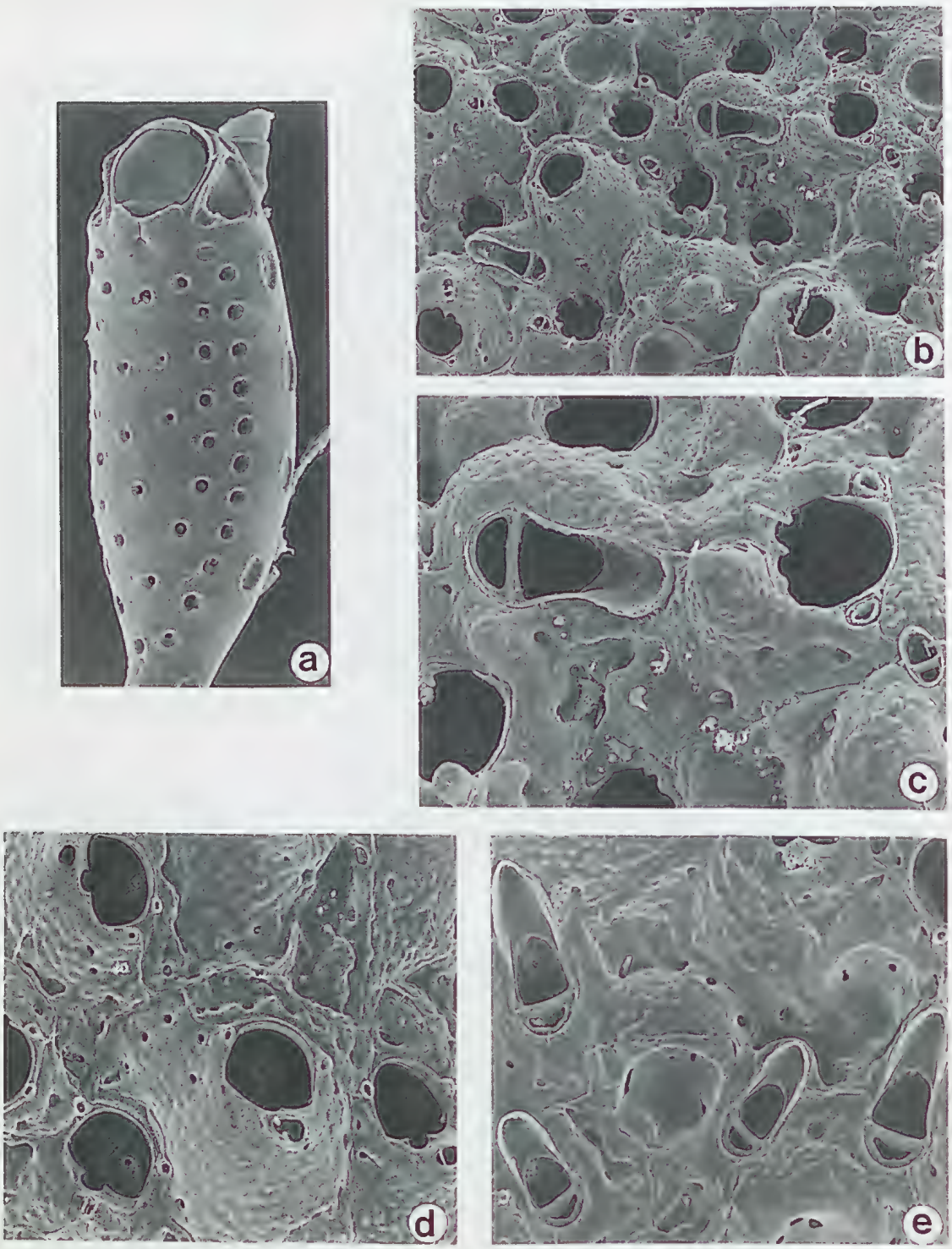


FIG. 14. a, *Vasignyella otophora*, ×120. b, c, *Celleporaria tridenticulata*; b, ×50; c, detail to show primary orifice and a vicarious avicularia, ×120. d,e, *Celleporaria aperta*; d, ×85; e, vicarious avicularia, ×95.

sheet. Autozooids 0.6-0.7×0.4-0.5mm; frontal wall convex, finely nodular or wrinkled, with few, relatively large, marginal pores. Primary orifice wider than long, about 0.12×0.17mm, the proximal border gently concave, bearing three denticles within its edge: lateral denticles stout, pointed; median denticle variable, quadrate, or anvil-shaped, its free edge often notched or bifid, sometimes completely divided to give two separate, slender denticles. No oral spines. Peristome developing early in ontogeny, enclosing and obscuring proximal and lateral borders of orifice; a single median suboral avicularium, columnar, the rostrum perpendicular to plane of orifice, elongate triangular, about 0.15mm long, with finely toothed distal edge; crossbar slender, with a conspicuous columella; apically, the avicularium is produced as a tapered umbo. Adjacent to the proximal end of the avicularium, the peristome is deeply notched. Tiny adventitious avicularia, with oval rostrum, often frequent along margins of autozooids. Vicarious avicularia rare, apparently absent from many colonies; small, rostrum 0.15-0.25mm long, parallel-sided, deeply cupped distally. Ovicell a simple hemisphere, widely open frontally, lightly calcified, but thickening slightly in later ontogeny.

REMARKS

This species is distinguished from *C. tridenticulata* by its large, columnar suboral avicularium, deep peristome, and lack of oral spines. *C. vagans* (q.v.) has three thin, pointed denticles within the proximal edge of the orifice; its suboral avicularium is proportionately much smaller than that of *C. desperabilis*, and the ovicell larger, with a granular surface, and an asymmetrical aperture which may bear a small avicularium on its rim.

Celleporaria fusca (Busk)
(Fig. 15a-d)

Cellepora fusca Busk, 1854: 88, pl. 119, fig. 2; pl. 120, fig. 6.
Celleporaria fusca: Harmer, 1957: 680, pl. 43, figs 1-7.

DESCRIPTION

Colony forming massive, nodulated, multilaminar sheets, often exceeding 25cm^2; less frequently, developing erect, irregularly branching growths; deep purplish-brown in colour. Aperture about as wide as long, more or less D-shaped, the proximal border slightly concave, and arched frontally. No oral spines. Peristomial thickening most pronounced proximally, incorporating a single medio-proximal avicularium, vertically orientated with respect to the aperture, its cystid produced apically as a stout, pointed umbo; rostrum facing laterally, small and oval (0.05mm long), or longer (0.15-0.30mm), with a strongly denticulate distal edge. Vicarious avicularia generally infrequent, but characteristic: rostrum slender, lanceolate, rounded distally and often with a slight lateral curve; 0.2-0.6mm long. Ovicell spherical, imperforate, its orifice rim with an asymmetrical thickening which may include a small adventitious avicularium. Immediately below the avicularium the peristome rim bears a narrow notch, on the other side of which the rim is slightly thickened.

REMARKS

Winston & Heimberg (1986) indicated that Harmer's (1957) account of *C. fusca* was founded on a number of similar, deeply pigmented species. Harmer's figures, however, appear to represent true *C. fusca*. The type specimen (BMNH reg. no. 1854.11.15.180) is labelled 'pl. 119. Cape Capricorn' in Busk's hand, although the published type locality was given as Bass' Strait. A second Busk collection specimen (BMNH 1899.7.1.4867A) is labelled 'Bass' Strait'; both this and the type specimen are labelled 'R', for HMS Rattlesnake. A Hincks collection specimen from Bass' Strait (BMNH 1899.5.1.1316), Torres Strait specimen figured by Harmer (1957)(BMNH 1963.9.8.11), and a Siboga specimen from Makassar (BMNH 1963.9.8.14 part) have all been compared with the two Busk collection specimens, and with the present series from Heron Island, and it is clear that they all represent a single species. On the basis of these specimens, *C. fusca* can be said to range along the entire east coast of Australia, from Bass Strait to Torres Strait, and into the Indo-Malaysian Archipelago. In view of Winston & Heimberg's (1986) account, the synonymy constructed by Harmer should be viewed with caution, until records from the Indian Ocean can be re-examined.

Celleporaria pigmentaria (Waters)
(Fig. 16d,e)

Holoporella pigmentaria Waters, 1909: 163, pl. 15, figs 16-19; pl. 16, figs 9-16; pl. 17, figs 22, 23.
Celleporaria pigmentaria: Harmer, 1957: 684, pl. 43, fig. 8; text- fig. 58.

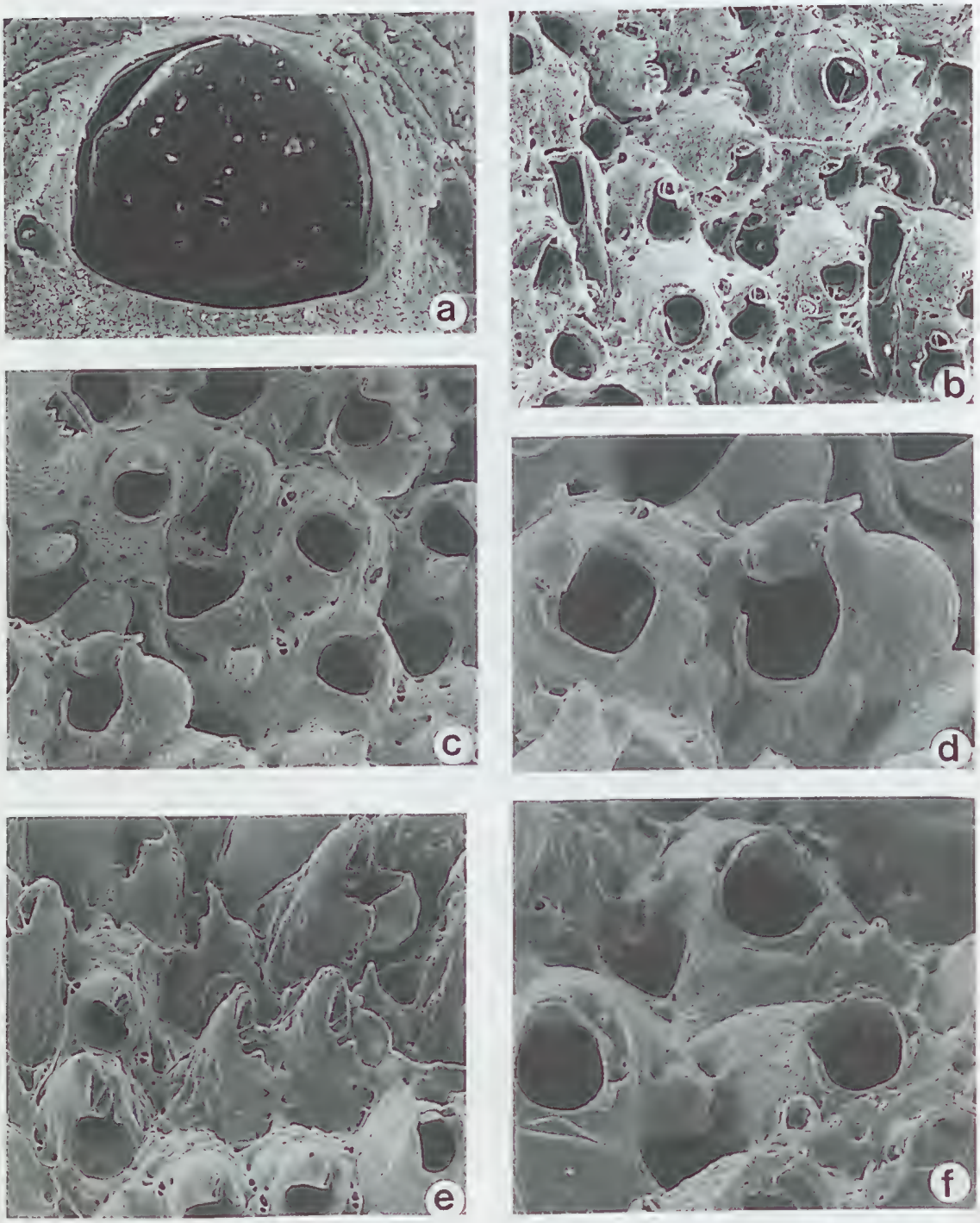


FIG. 15. a-d, *Celleporaria fusca*; a, primary orifice, ×290; b, part of colony, with elongate vicarious avicularia, ×45; c, part of colony, with spatulate vicarious avicularia, ×70; d, detail to show ovicell, ×120. e,f, *Celleporaria desperabilis*; e, ×55; f, ×100.

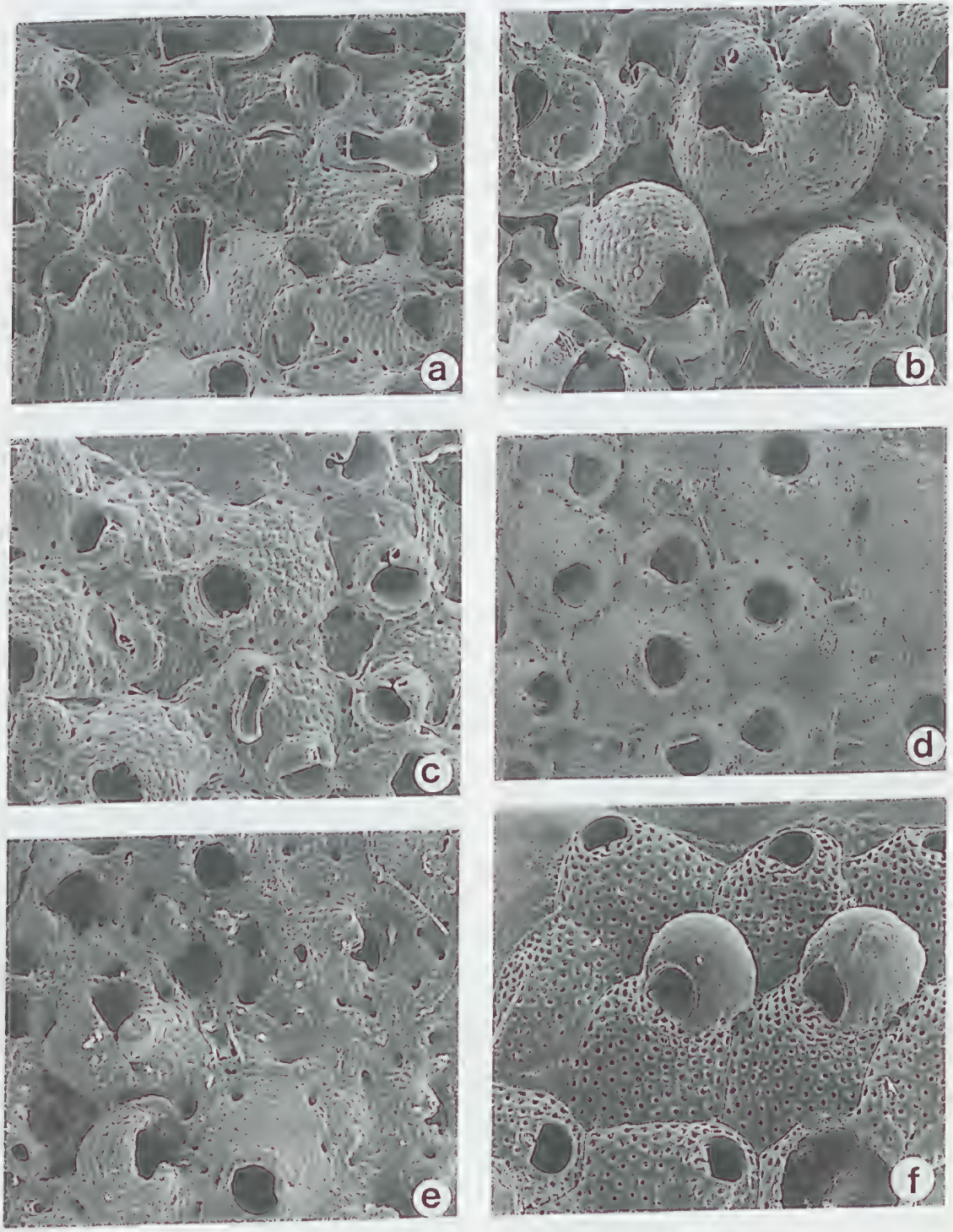


FIG. 16. a-c, *Celleporaria vagans*; a, ×45; b, ×50; c, ×45. d,e, *Celleporaria pigmentaria*; d, ×45; e, ×60. f, *Arthropoma cecilii*, ×50.

DESCRIPTION

Colony multilaminar, nodular, occasionally developing stout, erect, branching forms, deep brown to black. Autozooids oval, strongly convex, thickly calcified; commonly 0.5-0.6×0.4-0.5mm. Frontal wall coarsely nodular, with small, indistinct marginal pores. Aperture orbicular, slightly wider than long, its rim thickened but not especially prominent; a very small avicularium present mid-proximally, vertically orientated, with oval rostrum 0.05mm long; adjacent to the avicularium the peristomial rim clearly notched. No oral spines. Vicarious avicularia rare, usually absent; rostrum narrowly scaphoid, 0.25mm long, with incomplete crossbar. Peristomial avicularium occasionally giving rise to a stout, spiked mucro, which may be particularly accentuated among the oldest autozooids. Ovicell hemispherical, thickly calcified, inconspicuous.

REMARKS

This species was originally described from the Red Sea (Waters, 1909), and reported from a single Indonesian locality by Harmer (1957). The present material has been compared with the specimens from Ghardaqa and Sumbawa listed by Harmer, and with a specimen collected previously from Heron Island by L. Vail, and all seem to represent a single species.

Celleporaria vagans (Busk)
(Fig. 16a-c)

Cellepora vagans Busk, 1881: 343; 1884: 198, pl. 29, fig. 10; pl. 35, fig. 11.
Celleporaria vagans: Harmer, 1957: 671, pl. 42, fig. 4; text-fig. 55.

DESCRIPTION

Colony forming a multilaminar, encrusting sheet. Autozooids 0.6-0.8×c.0.4mm; frontal wall convex, nodular and rugose, bordered by small but distinct marginal pores. Primary orifice wider than long, commonly 0.17×0.12mm; proximal edge shallowly concave, with three thin, pointed denticles evenly spaced just within its rim. No oral spines. Peristome deep, developing in early ontogeny, enveloping lateral and proximal borders of orifice; a single median suboral avicularium, small, columnar, its apex produced as a short, pointed umbo; rostrum 0.1-0.2mm long, oval, orientated vertically to orifice plane and directed laterally. Peristome rim deeply notched adjacent to the proximal end of the avicularium; in later ontogeny a process extending from the peristome rim eventually fuses with the opposite rim, below the avicularium, to delimit a rounded spiramen. Vicarious avicularia infrequent, variable in length, but reaching 0.6mm; elongate, narrowest medially, spatulate and slightly cupped distally. Ovicell more than a hemisphere, overarching the primary orifice, surface finely granular, with a few indistinct perforations; its aperture irregularly triangular, the rim often peaked medially, and bearing a small avicularium in later ontogeny.

DISTRIBUTION

C. vagans is known from Hawaii, Torres Strait, Indonesia, and the eastern Indian Ocean, but from relatively few specimens. Busk's (1881, 1884) material from Crozet Island perhaps represents a different species, and requires re-examination.

Superfamily SCHIZOPORELLOIDEA Jullien, 1883
Family HIPPOPODINIDAE Levinsen, 1909

Colony encrusting. Autozooids with cryptocystidean frontal wall, evenly perforated. Orifice more or less bell-shaped: arched distally, shallowly concave proximally, with prominent lateral condyles. No oral spines. Avicularia adventitious, typically associated with orifice. Ovicell partly or wholly immersed, perforated, closed by autozooid operculum.

Hippopodina Levinsen, 1909

Colony encrusting. Frontal wall of autozooid with cryptocystidean development, perforated by numerous, closely spaced, small pores. Primary orifice bell-shaped; proximal border shallowly concave between distinct lateral condyles; no oral spines. Avicularia adventitious. Ovicell partially immersed in next autozooid, finely perforate, closed by autozooidal operculum. Vertical walls of autozooids with numerous, small, uniporous septula.

Type species: *Lepralia feegeensis* Busk, 1884.

Hippopodina feegeensis (Busk)
(Fig. 17a)

Lepralia feegeensis Busk, 1884: 144, pl. 22, figs 9, 9a, 9b.
Hippopodina feegeensis: Harmer, 1957: 974, pl. 67, figs 7-9; Winston & Heimberg, 1986: 16, figs 28-30.

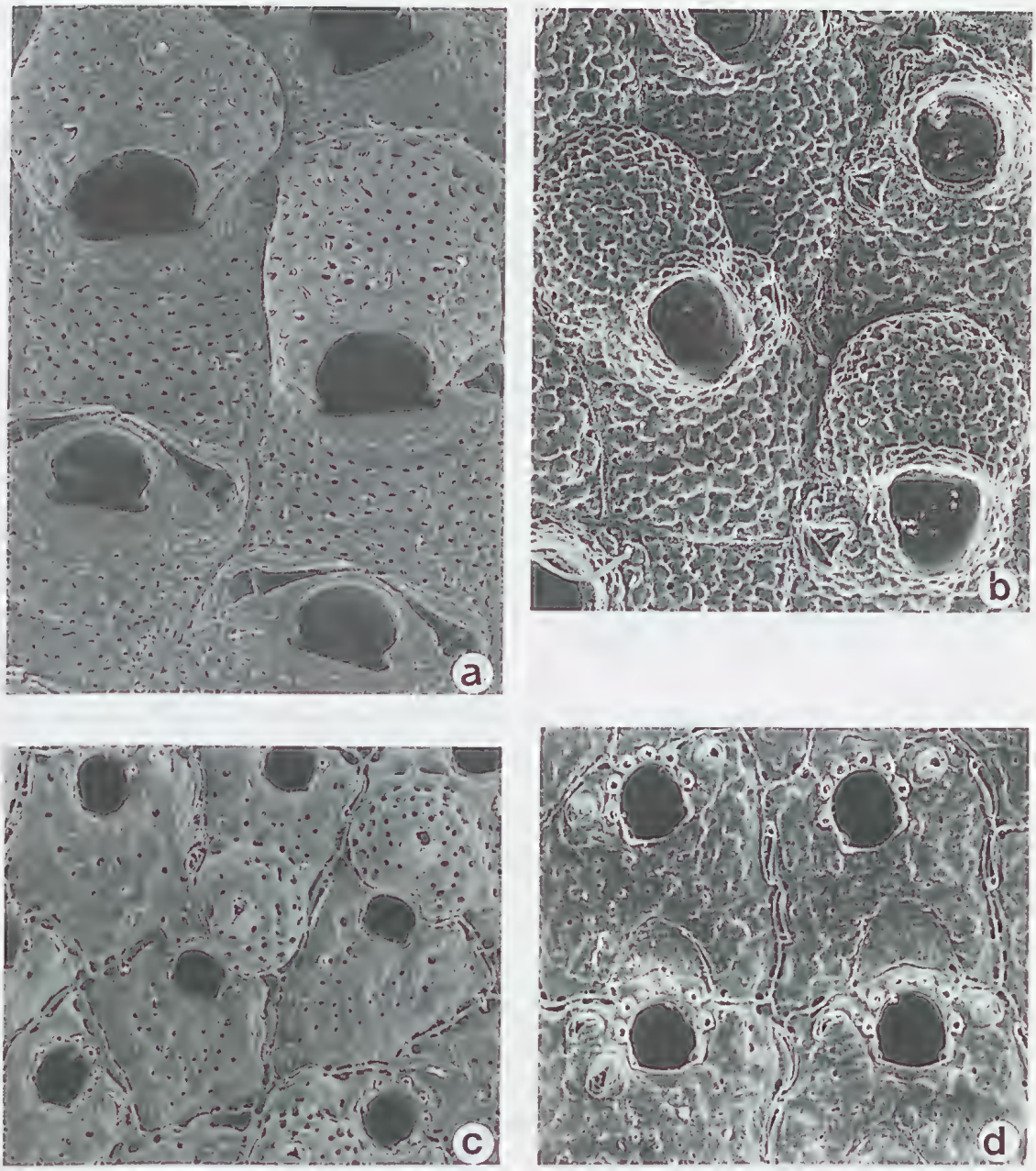


FIG. 17. a, *Hippopodina feegeensis*, ×55. b, *Cosciniopsis lonchaea*, ×50. c, d, *Thornelya perarmata*; c, ×60; d, ×85.

DESCRIPTION

Colonies forming thin, very extensive, light yellowish-brown, unilaminar sheets, glistening when dried. Autozooids oval to hexagonal, convex, separated by distinct grooves, lightly calcified; commonly 0.75-0.9×0.5-0.6mm. Primary orifice longer than wide, bell-shaped, with sharp, down-curved condyles. Frontal wall pearly or nodular, with numerous, densely-spaced, small pores, giving a speckled appearance at low magnification. Avicularia single or paired, disto-lateral to orifice; slender, acuminate rostrum directed medially, close to the distal border of the orifice.

Ovicell elongate oval, very prominent, densely perforated, with arched aperture.

REMARKS

H. feegeensis has a pan-tropical distribution in shallow waters. It forms broad flat sheets, often exceeding 100cm^2, on all kinds of hard substrata, and may be the most abundant bryozoan occurring on coral rubble in reef flat habitats. It is also often the primary colonising species on artificial substrata. It was common in 11 of the samples from Heron Island reported here.

Cosciniopsis Canu & Bassler, 1927

Colony encrusting, often strikingly pigmented. Autozooids large, robust, with thickly calcified, tuberculate frontal wall, pierced by numerous small pores. Primary orifice elongate-oval or bell- shaped, the proximal border broadly concave, between distinct lateral condyles. No oral spines. A well developed peristome typically present. Adventitious avicularia developed lateral to orifice, single or paired; lacking in some species. Ovicell hyperstomial, globular, with tuberculate calcification pierced by numerous small pores; closed by autozooid operculum.

Type species: *Cosciniopsis coelatus* Canu & Bassler, 1927.

Cosciniopsis lonchaea (Busk)
(Fig. 17b)

Lepralia lonchaea Busk, 1884: 146, text-fig. 43.
Cosciniopsis lonchaea: Harmer, 1957: 1083, pl. 72, figs 16, 17, 19, 20.

DESCRIPTION

Colony forming small, unilaminar patches. Autozooids oval to hexagonal, strongly convex, separated by deep grooves; 0.7-1.0×c.0.6mm. Primary orifice elongate-oval, the proximal edge with thickened, concave rim; condyles small and rounded; enveloped distally and laterally by a thin, raised peristome. Frontal calcification strikingly tuberculate, the tiny pores just visible between the tubercles. Most autozooids with a single, lateral-oral, avicularium; its blister-like cystid closely applied to the peristome, the acuminate rostrum acute to frontal plane, directed disto-medially towards the orifice. In some autozooids the lateral-oral avicularium is paired, one each side of the orifice; in others an identical avicularium occurs on the distal edge of the peristome, with the rostrum perpendicular to the frontal plane, directed towards the orifice of the autozooid. Ovicell slightly wider than long, globular, with tuberculate calcification and fine perforation identical to that of the autozooid.

DISTRIBUTION

Described originally from New Guinea, *C. lonchaea* has been reported from Torres Strait and South China Sea by Kirkpatrick (1890a,b) and from Indonesia by Harmer (1957). Waters (1909) recorded it from Sudan, while Harmer's (1957) synonymy of *Lepralia vestita* Hincks extends its range to Tahiti and Hawaii.

Thornelya Harmer, 1957

Colony encrusting, unilaminar. Primary orifice of autozooid bell-shaped, with broad, concave proximal border; condyles distinct; oral spines present. Frontal wall with large marginal pores, and small, scattered frontal pores. Adventitious avicularia present, often numerous, one to four per autozooid, most usually associated with the orifice or the ovicell, generally rather small. Ovicell recumbent on next autozooid, prominent, irregularly rounded, surface densely perforated, sutured, often bearing avicularia; closed by autozooid operculum.

Type species: *Lepralia ceylonica* Thornely, 1905.

Thornelya perarmata Harmer, 1957
(Fig. 17c,d)

Thornelya perarmata Harmer, 1957: 1105, pl. 73, figs 6-8.

DESCRIPTION

Colony forming very small, unilaminar patches. Autozooids irregularly rectangular to hexagonal, rather flat, separated by thickened sutures; 0.4-0.5×0.3-0.35mm. Primary orifice 0.12mm long, with six spines in a distal arc; condyles rounded, distinct. Frontal wall smoothly calcified, nodular; with 10-30 small pores centrally, and a single series of larger, elongate oval marginal pores. Avicularium single or paired, lateral to orifice; rostrum triangular, 0.1mm long, acute to frontal plane, directed towards orifice; one or two, occasionally more, avicularia developing in later ontogeny on distal edge of orifice, with rostrum directed towards it; additional avicularia developed along lateral margins of autozooids. Ovicell about as wide as long, prominent, with densely punctured, nodular surface; a single avicularium present on frontal surface, with rostrum proximally directed.

DISTRIBUTION

This species was described by Harmer (1957) from 141m off Waigeo Island, northwest New Guinea. It has not been recorded previously from the Great Barrier Reef, or from reef flat habitats. It seems to be common at Heron Island, and occurred in seven of the samples studied.

Family HIPPOPORINIDAE Brown, 1952

Colony encrusting; or erect with an encrusting base. Autozooids with regularly perforated frontal wall. Primary orifice shallowly concave proximally, or distinctly sinuate, with conspicuous condyles; no oral spines. Avicularia adventitious. Ovicell typically large, inflated, often sutured; in some genera brooding autozooids with large, dimorphic orifice.

Calyptotheca Harmer, 1957

Colony encrusting; sheet-like; or erect, bilaminate, plate-like. Frontal wall of autozooids densely perforated. Primary orifice sinuate, or with evenly concave proximal edge; dimorphic, typically larger and broader in brooding autozooids. Avicularia typically small, adventitious, lateral oral or sutural; rarely, vicarious; or absent. Ovicell large and conspicuous, perforated, closed by autozooid operculum.

Type species: *Schizoporella nivea* var. *wasinensis* Waters, 1913.

Calyptotheca tenuata Harmer
(Fig. 18b,c)

Calyptotheca tenuata Harmer, 1957: 1016, pl. 68, figs 16, 17.

DESCRIPTION

Colony developing extensive, multilaminar sheets. Autozooids oval to hexagonal or irregularly polygonal, convex, separated by thin, raised sutures; commonly 0.6-0.7×0.5mm. Primary orifice slightly wider than long, proximal border shallowly concave between knob-like proximo-lateral condyles; with a low, nodular peristome developing in later ontogeny. Frontal wall thick, densely and evenly perforated by regular, round pores, with nodular calcification between. Ovicell partly immersed in distally succeeding autozooid, wider than long, rather flattened frontally, with a coarsely nodular surface perforated by irregular pores. Avicularia sparse, developed on lateral margin of autozooid, proximal to orifice, directed medially and reaching midpoint of frontal wall; rostrum slender, acuminate, 0.35mm long.

DISTRIBUTION

C. tenuata was known only from Indonesia, the Loyalty Islands and Sri Lanka; Heron Island provides the first Australian record.

Calyptotheca thornelyae Dumont
(Fig. 18a)

Lepralia subimmersa: Thornely, 1905: 122.

[not] *Lepralia subimmersa* MacGillivray, 1879: 23, pl. 35, fig. 5.

Calyptotheca thornelyae Dumont, 1981: 625.

DESCRIPTION

Colony forming extensive, unilaminar or multilaminar, light reddish-brown sheets. Autozooids rectangular, hexagonal or irregularly polygonal, convex, separated by distinct sutures; 0.5-0.75×0.3-0.5mm. Primary orifice wider than long, proximal border shallowly and evenly concave between low, rounded, proximo-lateral condyles. Frontal wall thick, finely nodular, evenly perforated by numerous, small, round pores; a low, crenulate, peristomial rim characteristically present proximal to the orifice. Ovicell prominent, domed, occupying most of the frontal wall of the distally succeeding autozooid; calcification and perforation identical to that of autozooid frontal wall; orifice of brooding zooid shorter than that of autozooid, with more shallowly concave proximal edge. Adventitious avicularia sporadic, infrequent; 0.1mm long, with slender, acuminate rostrum; single or paired, most usually situated proximo-lateral to orifice, medially directed, occasionally budded along the lateral margins of autozooids in later ontogeny.

REMARKS

Thornely's (1905) two specimens of '*Lepralia subimmersa*' from Sri Lanka appear to be the only known material of this species, prior to its collection from Heron Island; one of the specimens was designated lectotype of *Calyptotheca thornelyae* by Dumont (1981). Both specimens have been compared with the Heron Island material, and there is no doubt that the two sets are conspecific. *Calyptotheca subimmersa* (MacGillivray) is presently known only from the southern coasts of Australia.

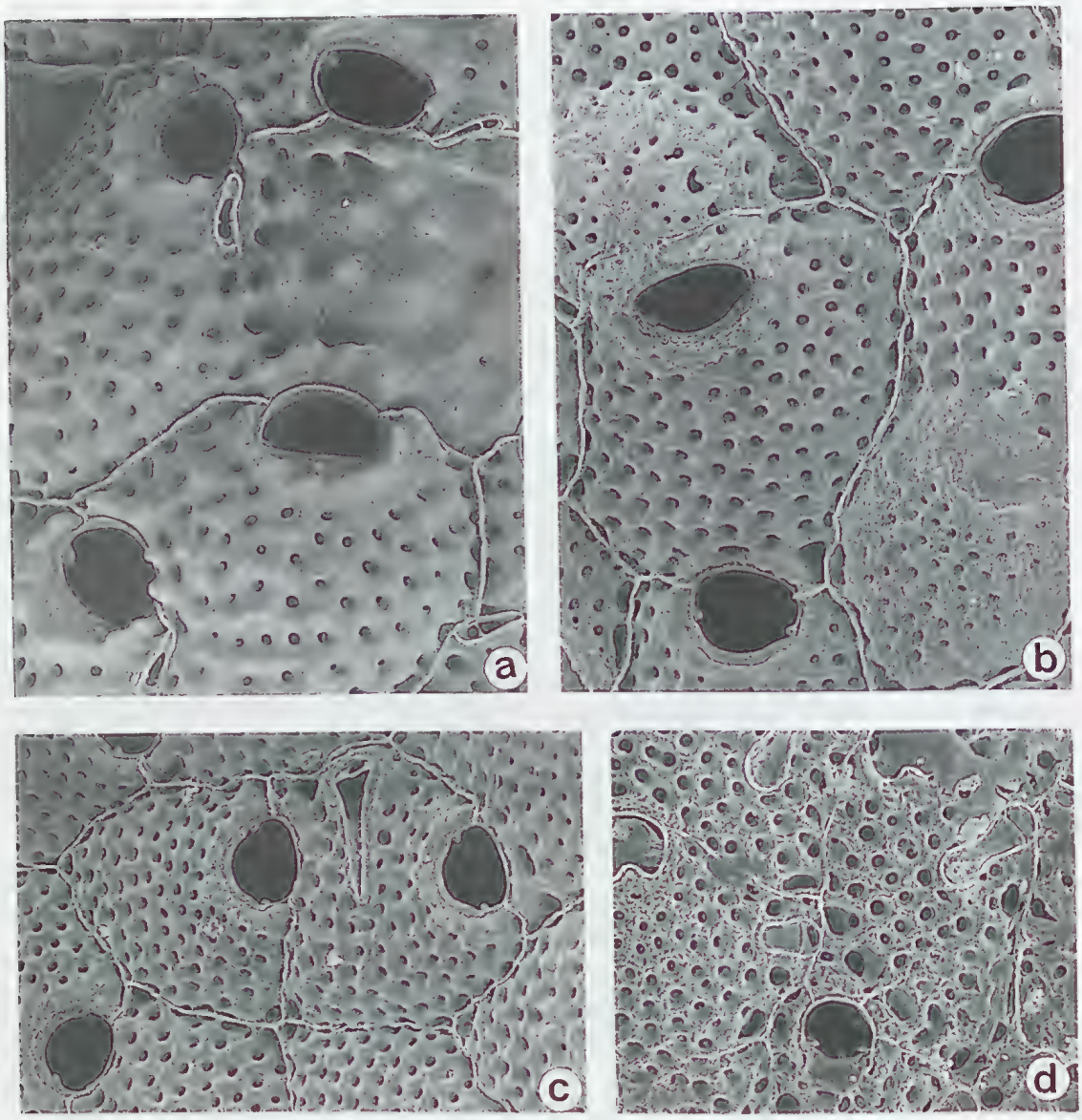


FIG. 18. a, *Calyptotheca thornelyae*, ×90. b,c, *Calyptotheca tenuata*; b, ×70; c, ×60; d, *Emballotheca pacifica*, ×70.

Emballotheca Levinsen, 1909

Colony encrusting. Autozooids with evenly perforated frontal wall. Primary orifice shallowly concave proximally, or distinctly sinuate; with well-marked condyles; dimorphic, larger and broader in brooding autozooids. No oral spines. Avicularia adventitious; or absent. Ovicells large, inflated, sutured; regularly porous.

Type species: *Eschara quadrata* MacGillivray, 1880.

Emballotheca pacifica Harmer
(Fig. 18d)

Emballotheca pacifica Harmer, 1957: 1088, pl. 67, figs 3-5.

DESCRIPTION

Colony an encrusting, multilaminar sheet. Autozooids rectangular to irregularly polygonal, convex, separated by distinct sutures. Primary orifice wider than long, its proximal border with

a rounded-triangular median process; with large, downcurved lateral condyles. Frontal wall thick, coarsely granular, perforated by large, irregular pores, which tend to fuse in later ontogenetic thickening. Ovicell prominent, obscuring much of distally succeeding autozooid, as wide as long, surface granular and coarsely perforated, and typically crossed by sutures; the orifice of ovicelled autozooids is broader than that of ordinary autozooids, with a shallowly concave proximal edge. Avicularia situated proximo-lateral to orifice, directed proximo-medially; of variable length, up to 0.3mm long; the smallest with a semielliptical mandible, the largest distinctly spoon-shaped.

DISTRIBUTION

Previously from isolated localities in the western Pacific, from the South China Sea to Torres Strait.

Robertsonidra Osburn, 1952

Colony encrusting. Autozooids with tuberculate frontal wall, bordered by conspicuous marginal pores. Primary orifice with proximal sinus, frequently with a pronounced lateral suboral umbo; spines present or absent. Avicularia adventitious. Ovicell hyperstomial, closed by autozooid operculum; surface tuberculate, with minute perforations. Vertical walls with very small uniporous septula; basal walls typically raised above the substratum on stout, projecting processes.

Type species: *Schizoporella oligopus* Robertson, 1908.

Robertsonidra argentea (Hincks)
(Fig. 19b)

Schizoporella argentea Hincks, 1881b: 158, pl. 9, figs 6, 6a.

Rhamphostomella argentea: Harmer, 1957: 1102 [part-tim].

[not] *Robertsonidra argentea*: Powell, 1967: 169.

Colony a small, yellowish-white patch; unilaminar. Autozooids oval to broadly hexagonal, convex, separated by distinct sutures; 0.6-0.75×0.4-0.5mm. Primary orifice about as long as wide; proximal edge deeply, symmetrically concave, lacking condyles; two or three, thin, evanescent spines present in early ontogeny; frequently a short, asymmetrically-placed suboral umbo. Frontal wall regularly tuberculate, with a single row of round marginal pores. Avicularia dimorphic, one or both types present on a single autozooid, some autozooids without either; lateral-suboral, acute to frontal plane, laterally directed, with short, hooked rostrum, or normal to frontal plane, proximo-laterally directed, with elongate triangular rostrum. Ovicell spherical, regularly tuberculate, with minute perforations.

OCCURRENCE

A single specimen collected from Heron Island, Stn 23, encrusting coral rock, constitutes the first Australian record.

REMARKS

Harmer's (1957) account of *R. argentea* was based on several different species, and there is no indication that he examined either the type specimen (BMNH reg.no. 1899.5.1.970, loc. 'Africa') or material of the genus type, *Schizoporella oligopus* Robertson, which he placed in the synonymy of *R. argentea*. Two of the Siboga specimens listed by Harmer (1957:1101) have been compared with the type specimen of *R. argentea* and found to represent two different, undescribed, species of *Robertsonidra*. Specimen 399D (Stn 164, BMNH reg.no. 1975.7.24.22) has a pear- shaped orifice with three distal oral spines and a disto- laterally orientated, lateral suboral avicularium, with an elongate triangular rostrum; the autozooids are only loosely coherent. Specimen 108F (Stn 144, BMNH reg.no. 1975.2.24.14) has a transversely oval orifice with a distinct U-shaped sinus, lacks spines, and has a distally-directed, lateral-suboral avicularium with a short, broadly triangular rostrum. Powell's (1967) figure of '*R. argentea*' from the southern Red Sea depicts yet another species of *Robertsonidra*, *R. oligopus*, which is known from the Galapagos Islands and Southern California is almost certainly distinct from *R. argentea*, and from any of the other species discussed here. The type locality of *R. argentea* is unknown, although its habitat, 'on coral', suggests it lies somewhere on the East African coast.

Robertsonidra novella sp. nov.
(Fig. 19a)

TYPE MATERIAL

HOLOTYPE: GH5230, Heron Island, Stn 22, 15 Apr 1972.

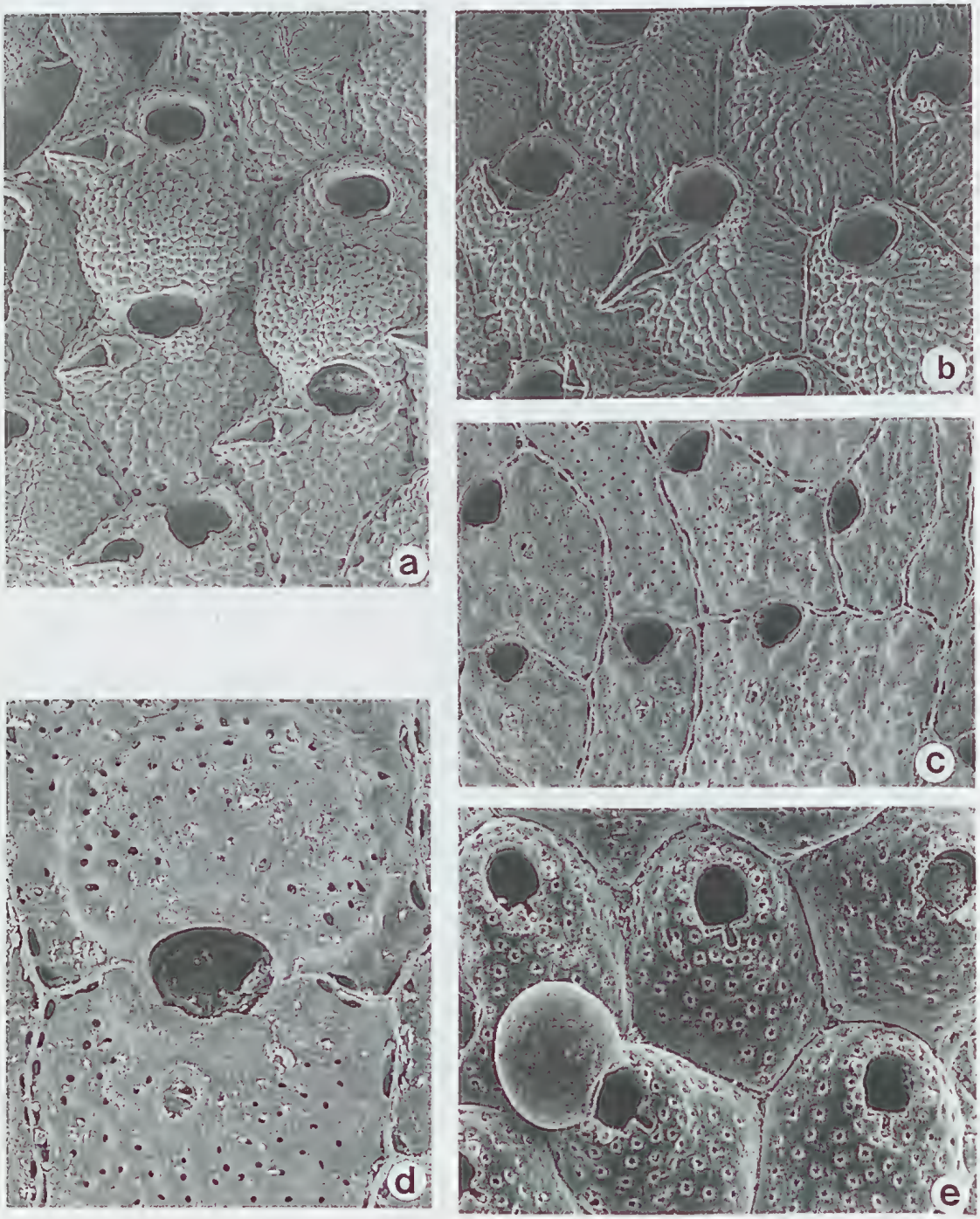


FIG. 19. a, *Robertsonidra novella*, ×60. b, *Robertsonidra argentea*, ×60. c,d, *Schizomavella inclusa*; c, ×70; d, ×140. e, *Phonicosia circinata*, ×70.

ETYMOLOGY
Latin *novella*, diminutive of *novus*, new.

DESCRIPTION
Colony forming small, silvery, unilaminar patches. Autozooids oval to hexagonal, strongly convex, separated by distinct grooves; 0.5-0.6×0.35-0.4mm. Primary orifice transversely oval, proximal border with a short, U-shaped sinus flanked by small condyles; one or two short, evanescent spines present distally, their bases persisting especially in ovicelled autozooids; a short umbo situated lateral to the sinus in many autozooids. Frontal wall regularly tuberculate, glistening under low magnification, with a single series of round marginal pores. Avicularia sporadic, lateral suboral; rostrum elongate triangular, directed proximo-laterally. In some autozooids a second, shorter avicularium occurs lateral to the sinus, with the rostrum acute to frontal plane and laterally directed. Ovicell slightly wider than long, globular, the surface tuberculate, with minute perforations between the tubercles.

REMARKS
This species is distinguished from *R. argentea* by its oval orifice, which has a distinct proximal sinus bounded by small condyles. It was present in three of the Heron Island samples.

Family SCHIZOPORELLIDAE Jullien, 1883

Colony encrusting or erect. Autozooids with cryptocystidean frontal wall; evenly perforated or with marginal pores only. Primary orifice typically with distinct proximal sinus and conspicuous condyles; oral spines present or absent. Avicularia adventitious and/or vicarious or interzooidal; or absent. Ovicells present. Vertical walls with basal pore chambers or mural septula.

Schizomavella Canu & Bassler, 1917

Colony encrusting. Frontal wall of autozooid with regularly distributed perforations. Primary orifice with distinct sinus and well-marked condyles; oral spines present or absent. Avicularia adventitious, typically suboral, but also lateral-oral, or frontal; dimorphic in some species. Ovicell hyperstomial, variably perforate, closed by autozooidal operculum. Vertical walls with small septula.

Type species: *Lepralia auriculata* Hassall, 1842.

Schizomavella inclusa (Thornely)
(Fig. 19c,d)

Schizoporella inclusa Thornely, 1906: 450.
Schizomavella inclusa: Harmer, 1957: 1028, pl. 66, figs 4, 6, 7; Winston & Heimberg, 1986: 18, figs 43, 44.

DESCRIPTION
Colony forming thin, flat encrustations. Autozooids irregularly rectangular, flat, separated by distinct sutures; 0.35-0.5×0.25-0.35mm. Primary orifice as wide as long, broadest distally and appearing pear-shaped, with a deep, U-shaped proximal sinus below short, distinct condyles. No oral spines. Frontal wall thick and vitreous, irregularly nodular, with numerous, small, round pores; marginal pores larger and more distinct. Avicularium suboral, proximally directed, 0.05mm long, with oval or bluntly triangular rostrum. A dimorphic avicularium, with enlarged, spatulate mandible was described by Harmer (1957). Ovicell wider than long, partially immersed; with numerous small pores, most densely distributed around edges.

DISTRIBUTION
S. inclusa has been described from scattered localities, from Madagascar, Mauritius and Sri Lanka, to Indonesia, New Guinea and New Britain. Harmer (1957) recorded a specimen from the Red Sea, but it has not been recorded previously, with certainty, from Australian seas.

Arthropoma Levinsen, 1909

Colony encrusting. Autozooid with evenly perforated frontal wall. Primary orifice with narrow medio-proximal sinus; operculum articulated. No oral spines. Avicularia absent. Ovicell prominent, imperforate, closed by autozooid operculum. Vertical walls with large, multiporous septula. Ancestrula identical to later autozooids.

Type species: *Flustra cecilii* Audouin, 1826.

Arthropoma cecilii (Audouin)
(Fig. 16f)

Flustra cecilii Audouin, 1826: 239; Savigny pl. 8, fig. 3.
Arthropoma cecilii: Harmer, 1957: 1001, pl. 72, fig. 23; text- fig.108; Gordon, 1984: 85, pl. 30, fig. A.

DESCRIPTION

Colony forming small, glistening, white patches; usually unilaminar. Autozooids lightly calcified, strongly convex, with densely perforated frontal wall; commonly 0.5-0.7× 0.5mm. Primary orifice slightly wider than long, D-shaped, with a very narrow, medio-proximal sinus. No avicularia, although Harmer (1957) reports a polymorph with an operculum twice the size of that of ordinary autozooids. Ovicell prominent, convex, smoothly calcified, opaque white.

DISTRIBUTION

A. cecilii is widespread and common in all shallow, tropical, subtropical and warm temperate seas. It has been reported previously from reef habitats in the Caribbean, the Indian Ocean, the East Indies and the GBR.

Phonicosia Jullien, 1888

Colony encrusting. Autozooid frontal wall with conspicuous marginal pores, and sometimes with additional pores proximo-lateral to orifice, but with central area usually imperforate. Primary orifice with proximal sinus; operculum articulated; distal oral spines present. Adventitious avicularia occur sporadically. Ovicell prominent; ectooecium membranous; entooecium calcified; imperforate, except for small basal pores around periphery; not closed by autozooid operculum. Basal pore chambers present.

Type species: *Phonicosia jousseaumei* Jullien, 1888 [= *Lepralia circinata* MacGillivray, 1869].

Phonicosia circinata (MacGillivray) (Fig. 19e)

Lepralia circinata MacGillivray, 1869: 134.
Arthropoma circinatum: Harmer, 1957: 1003, pl. 72, figs 29-30; Hayward & Cook, 1983: 69, fig. 17c.
Phonicosia circinata: Gordon, 1984: 87, pl. 30, figs E,F; 1989: 46.

DESCRIPTION

This distinctive species is readily recognized by its D-shaped orifice, with slit-like sinus and broad, denticulate condyles, surrounded by eight or nine spines.

DISTRIBUTION

P. circinata has a wide geographical distribution, ranging throughout the western Pacific Ocean, from Japan to New Zealand, eastwards to South Africa, Tristan da Cunha, the Patagonian Shelf and Tierra del Fuego; also at Marion Island and Kerguelen.

REMARKS

In some populations a large adventitious avicularium occurs proximal to the sinus, and the density and distribution of frontal wall pores also varies greatly. However, these variations may be observed over a relatively small geographic distance, and perhaps even within single populations.

Escharina Milne-Edwards,1836

Colony encrusting or erect. Frontal wall of autozooids with distinct marginal pores, and evenly scattered, minute perforations. Primary orifice with well marked sinus; oral spines present. Avicularia adventitious or interzooidal. Ovicell hyperstomial, imperforate, closed by autozooid operculum. Small basal pore chambers present.

Type species: *Eschara vulgaris* Moll, 1803.

Escharina pesanseris (Smitt)

Hippothoa pesanseris Smitt, 1873: 43, pl. 7, figs 159, 160 .
Escharina pesanseris: Harmer, 1957: 998, pl. 67, figs 12-14,18,19; Gordon, 1984: 84, pl. 29, figs A, B.

DESCRIPTION

Colony encrusting, forming small rounded patches; rather inconspicuous. Autozooids oval, convex; about 0.8×0.5mm; frontal wall finely granular, fine perforations revealed only by high magnification. Primary orifice longer than wide, with a narrow, slit-like sinus between broad condyles; with eight or nine stout distal oral spines, and a low proximal peristomial rim. Avicularia paired, lateral to orifice, with distinctive, duck's foot-shaped mandibles distally directed. Ovicell relatively small, wider than long, with a transverse frontal ridge; six spines only in ovicelled autozooids.

DISTRIBUTION

E. pesanseris has a circumtropical distribution in shallow water, and occurs commonly in reef habitats.

Stylopoma Canu & Bassler, 1920

Colony encrusting, multilaminar, developing

extensive nodular growths. Frontal wall of autozooids evenly perforated by small pores, with a marginal series of larger pores. Primary orifice with well developed condyles and deep proximal sinus; no oral spines. Avicularia adventitious, small, and vicarious, large. Ovicell globular, prominent, perforated; overhanging and eventually occluding orifice of brooding autozooid. Vertical walls with numerous, small, recessed septula.

Type species: *Eschara spongites* Pallas, 1766.

The genus *Stylopoma* has a pantropical distribution in shallow, coastal waters, and most species described seem to be commonly found in reef habitats. Most are brightly pigmented.

Stylopoma duboisii (Audouin)
(Fig. 20a,b)

Flustra?duboisii Audouin, 1826: 239; 1828: 66; Savigny pl. 8, figs 41, 42 .
Stylopoma duboisii: Harmer, 1957: 1033, pl. 74, figs 1-7; Winston & Heimberg, 1986: 20, figs 45-57.

DESCRIPTION

Autozooids irregularly polygonal, rather flat, separated by distinct sutures; 0.5-0.6×0.35-0.45mm. Primary orifice wider than long, D-shaped, the straight proximal border with a slit-like median sinus; condyles low and broad, occupying whole of proximal border on each side of sinus, distal edges finely toothed. Frontal wall densely perforated by small round pores, and with a single series of larger marginal pores; becoming coarsely nodular in later ontogeny. Typically, a single, small avicularium proximo-lateral to orifice, acute to frontal plane, disto-laterally directed; 0.05mm long, with short, triangular mandible. Additional avicularia may be budded in later ontogeny, especially in brooding autozooids, and most usually in proximity to the orifice. Vicarious avicularia infrequent, as large as autozooids, with broadly spatulate mandible. Ovicells globular, prominent, 0.5mm diameter, occupying the frontal surface of several adjacent autozooids; densely porous, with the aperture overhanging and obscuring the orifice of the maternal autozooid.

DISTRIBUTION

This species is common in shallow waters throughout Malaysia and Indonesia, and on the coasts of New Guinea and Queensland. It ranges westwards to Sri Lanka and the Red Sea, and was reported from West Africa by Cook (1968b). Seven of the Heron Island samples contained large colonies of *S. duboisii*.

Stylopoma thornelyae Livingstone
(Fig. 20c)

Schizoporella viridis var. *thornelyi* Livingstone, 1926: 84, pl. 8, figs 8, 9.

DESCRIPTION

Autozooids rectangular to polygonal, convex, separated by distinct sutures; 0.6-0.8×0.35-0.5mm. Primary orifice about as wide as long, proximal border with a broad V-shaped sinus occupying about half its width; condyles rectangular, distinct. Frontal wall densely perforated by small, evenly distributed pores, each in a shallow pit. A single, small adventitious avicularium present on many autozooids, lateral to sinus; rostrum 0.08mm long, acute to frontal plane, distally directed, supporting a short, triangular mandible. Vicarious avicularia sporadic, slightly smaller than autozooids, with waisted, spatulate rostrum.

DISTRIBUTION

This species is known with certainty only from the Great Barrier Reef, although part of the Indonesian material described by Harmer (1957) as *S. parviporosum* Canu & Bassler may represent *S. thornelyae*.

Stylopoma viride (Thornely)
(Fig. 20d)

Schizoporella viridis Thornely, 1905: 116, fig. 3.
Stylopoma viride: Harmer, 1957: 1036, pl. 74, figs 8-13; Winston & Heimberg, 1986: 21, figs 48-50.

DESCRIPTION

Autozooids rectangular, diamond-shaped or polygonal, convex, separated by distinct sutures; 0.8-1.2×0.5-0.6mm. Primary orifice orbicular, with a deep V-shaped sinus occupying two-thirds of the proximal width; condyles small, knob-like. Frontal wall densely perforated by small, round pores, the marginal series slightly larger and more distinct; calcification thick, forming raised, nodular ridges between the pores. Majority of autozooids with characteristic disto-lateral adventitious avicularium; rostrum slender, pointed, 0.35mm long, extending disto-medially above the orifice. A smaller suboral avicularium present in many autozooids, adjacent to sinus, with varying orientation. Vicarious avicularia identical to

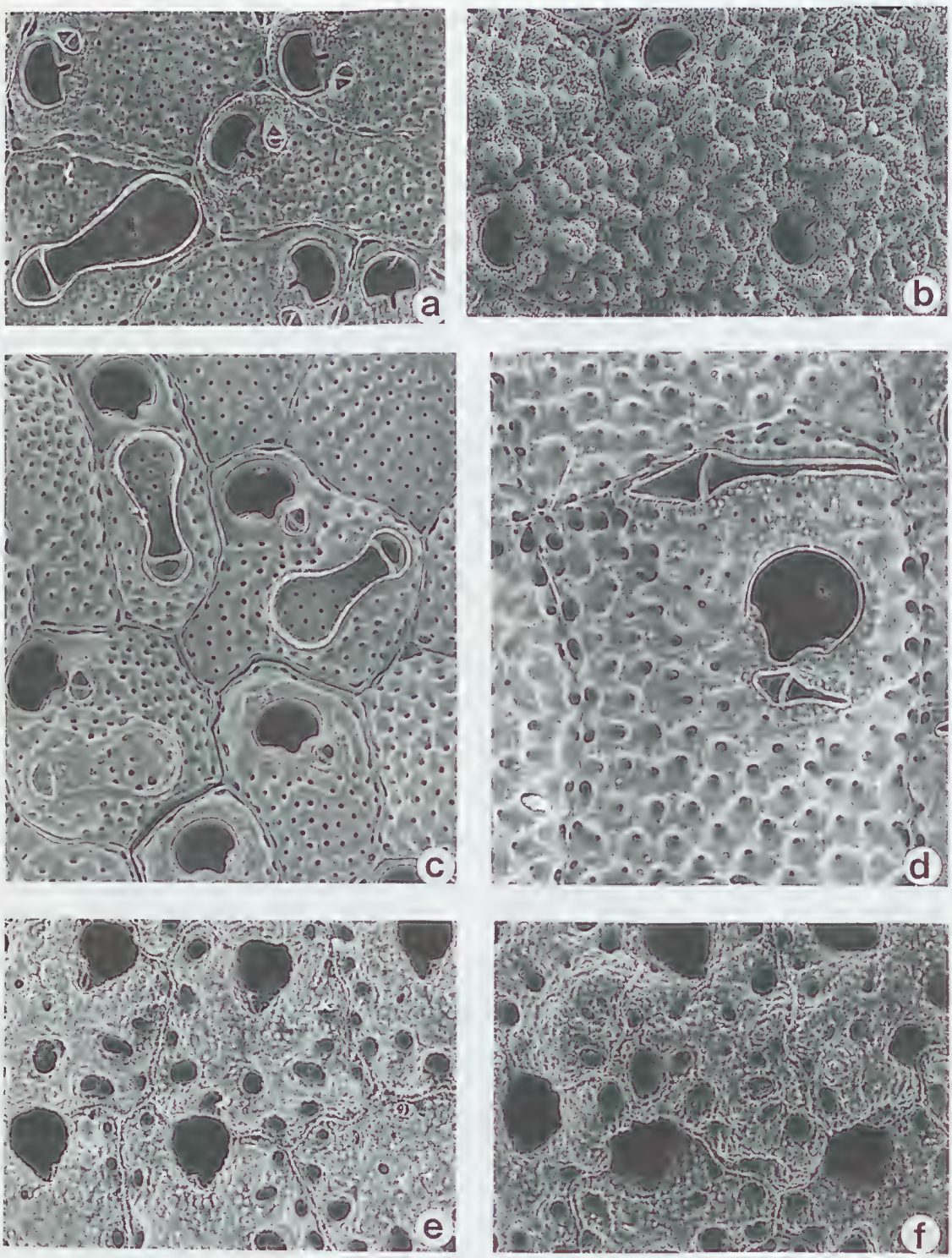


FIG. 20. a,b, *Stylopoma duboisii*; a, ×80; b, ×70. c, *Stylopoma thornelyae*, ×80. d, *Stylopoma viride*, ×80. e,f, *Cigclisula areolata*; e, autozooids, ×50; f, two ovicelled zooids, ×50.

disto-lateral adventitious avicularia; rare. Ovicell globose, as large as an autozooid, with identical calcification and perforation, and with an independent, frontally situated aperture.

REMARKS

The massive, multilaminar colonies of *S. viride* have a characteristic green coloration, muted in living colonies by a thick, greyish-brown frontal cuticle. The pigment is contained within the calcification and persists after the death of the colony.

DISTRIBUTION

This species is known from the Red Sea, Sri Lanka and other localities in the Indian Ocean; it has been widely reported from Malaysia, Indonesia, New Guinea and the Philippines, and is distributed on north and northeast coasts of Australia, and along the Great Barrier Reef.

Family STOMACHETOSELLIDAE Canu & Bassler, 1917

Colony encrusting, forming a thick, multilaminar sheet; or erect, as folded, bilaminar plates attached by an encrusting base. Autozooids thickly calcified; frontal wall with marginal and frontal pores. Primary orifice sinuate or bell-shaped, encircled by a deep, thick peristome. Avicularia adventitious and/or vicarious; or absent. Ovicells present, typically with few, large, frontal lacunae.

Cigclisula Canu & Bassler, 1927

Colony encrusting or erect, unilaminar or multilaminar, often nodular or massive. Frontal wall of autozooid with marginal perforations (sometimes in double or triple series), with stout interareolar ridges developing in later ontogeny; central area of frontal wall imperforate. Primary orifice more or less bell-shaped, the proximal border shallowly concave between distinct condyles. No oral spines. A thickened peristomial rim developing in later ontogeny, characteristically incorporating a proximal suboral avicularium, eccentrically placed and laterally directed. Additional small, adventitious avicularia may be present elsewhere on autozooid; in some species large, vicarious avicularia also occur. Ovicell characteristic: prominent, grossly inflated, sutured, with a few, large, frontal lacunae.

Type species: *Escharoides occlusa* Busk, 1884.

Cigclisula areolata (Kirkpatrick) (Fig. 20e,f)

Lepralia occlusa var. *areolata* Kirkpatrick, 1890a: 618, pl. 16, figs 7, 7a.
Porella areolata: Livingstone, 1926: 91, pl. 8, fig. 4.
Cigclisula areolata: Hastings, 1932: 434.

DESCRIPTION

Colony forming thick, extensive multilaminar sheets. Autozooids oval to hexagonal, strongly convex, thickly calcified, separated by distinct sutures; commonly 0.6-0.7 × 0.4-0.5mm. Primary orifice as wide as long, bell-shaped, with concave proximal border; condyles small, rounded. Frontal calcification coarsely granular, becoming distinctly nodular in later ontogeny, with a double or triple series of marginal pores, but the central area of the frontal wall imperforate. As the frontal wall thickens, stout ridges develop peripherally, eventually forming a series of large, deep areolae, each of which may enclose two or more of the original pores. Orifice encircled by a thick, peristomial rim; a single, small avicularium proximo-medially; its rostrum perpendicular to frontal plane and facing laterally, immersed in peristomial calcification, but with tip of rostrum hooked and distinct. Large vicarious avicularia occur sporadically. Ovicell wider than long, almost as large as autozooid, globular and prominent, with the aperture overhanging the autozooid orifice; bordered by large areolae, and with four to eight large lacunae frontally.

DISTRIBUTION

This species is known only from Torres Strait and the Great Barrier Reef. At Heron Island large colonies were present in two samples from reef crest locations.

Family SMITTINIDAE Levinsen, 1909

Colony encrusting or erect. Autozooids with cryptocystidean frontal wall, evenly perforated or with marginal perforations only. Primary orifice with or without a median proximal denticle (lyrula) and proximo-lateral condyles; oral spines present or absent. Avicularia adventitious, or absent. Ovicell prominent, perforate or imperforate.

Smittoidea Osburn, 1952

Frontal wall of autozooids with marginal pores only. Avicularium situated medially on the frontal wall, immediately proximal to the orifice,

often partly enveloped by the peristome; typically proximally directed. Ovicell prominent, evenly perforated. Vertical walls with mural septula.

Type species: *Smittoidea prolifica* Osburn, 1952.

Smittoidea pacifica Soule & Soule (Fig. 24e,f)

Smittoidea pacifica Soule & Soule, 1973: 380, figs I, F-H.

DESCRIPTION

Colony a small, silvery-white, unilaminar patch. Autozooids oval to hexagonal, flat or slightly convex, separated by indistinct sutures; 0.4-0.5×0.2-0.3mm. Primary orifice wider than long; lyrula anvil-shaped, broad and deep, occupying entire width of orifice; condyles short and blunt, indistinct. No oral spines. Peristome completely encircling orifice, its edge thickened and slightly lobed in later ontogeny; with a conspicuous U-shaped notch medio-proximally, the inner edges of which may be thickened to define a descending groove. Frontal wall coarsely nodular, bordered by large and conspicuous marginal pores. A single suboral avicularium on each autozooid, directed proximally or proximo-laterally; rostrum elongate, finely tapered, rounded at tip, its edges sometimes finely denticulate; crossbar thickened, the proximal opesia circular. Ovicell slightly wider than long, frontal surface with numerous small pores; developing a coarsely nodular ooecial cover, which extends to the distal edge of the peristome, leaving only the central frontal area of the ovicell exposed.

REMARKS

Soule & Soule (1973) founded this species on specimens collected from Hawaii. They included Osburn's (1952) record of *S. reticulata* (J. Macgillivray) from the Galapagos Islands in the synonymy of *S. pacifica*, while noting that one zooid in Osburn's specimen bore six oral spines. The Heron Island specimens here described have been compared with Hawaiian paratype material of *S. pacifica*, which they match exactly.

S. reticulata is distributed in the eastern Atlantic region from the Mediterranean to the Barents Sea, and almost certainly does not occur in the Pacific. Osburn's Galapagos material does not belong to *S. reticulata*, and is possibly not *S. pacifica* either.

Parasmittina Osburn, 1952

Colony encrusting, unilaminar or multilaminar. Frontal wall of autozooid with marginal pores only. Primary orifice with medio-proximal lyrula and paired lateral condyles; oral spines usually present; typically with a well developed peristome. Avicularia adventitious and interzooidal, frequently polymorphic, often numerous; characteristically, one or more occur lateral to the orifice. Ovicell hyperstomial, prominent, with frontal pores; not closed by autozooid operculum. Small basal pore chambers present.

Type species: *Lepralia jeffreysi* Norman, 1876.

Species of *Parasmittina* are common, and often abundant, in shallow reef habitats. Species diversity is usually high (e.g., Soule & Soule, 1973; Hayward, 1988) and it is probable that many tropical species remain to be recognized.

Parasmittina hastingsae Soule & Soule (Fig. 21a-c)

Parasmittina hastingsae Soule & Soule, 1973: 417, figs 9C,D.

Parasmittina hastingsae: Winston & Heimberg, 1986: 26, figs 59-63.

DESCRIPTION

Colony forming broad, yellowish, multilaminar sheets. Autozooids oval, hexagonal or irregular, convex, separated by distinct sutures; commonly 0.35-0.5×c.0.25mm. Primary orifice slightly wider than long, rounded; lyrula occupying about half proximal orifice width, with convex edge and bluntly pointed corners; condyles acute, distinct. Two or three (rarely four) short, distal oral spines present in early ontogeny; peristome developed as paired lateral folds, with a deep, medio-proximal sinus between; erect and slightly flared, enclosing distal border of orifice in later ontogeny. Frontal wall of autozooid finely nodular, with a single series of round marginal pores. As calcification thickens in later ontogeny, the boundaries between individual autozooids become increasingly obscure, and the marginal pores much more irregular in outline. Avicularia of three main types, all becoming more frequent in later ontogeny: most characteristically a short, oval type, proximo-lateral to orifice, proximally directed; less frequently, a larger type with rostrum elongate, tapered, rounded distally and serrated along its edge, directed proximally; finally, a large interzooidal type with rostrum tapered, rounded and slightly flared distally, its

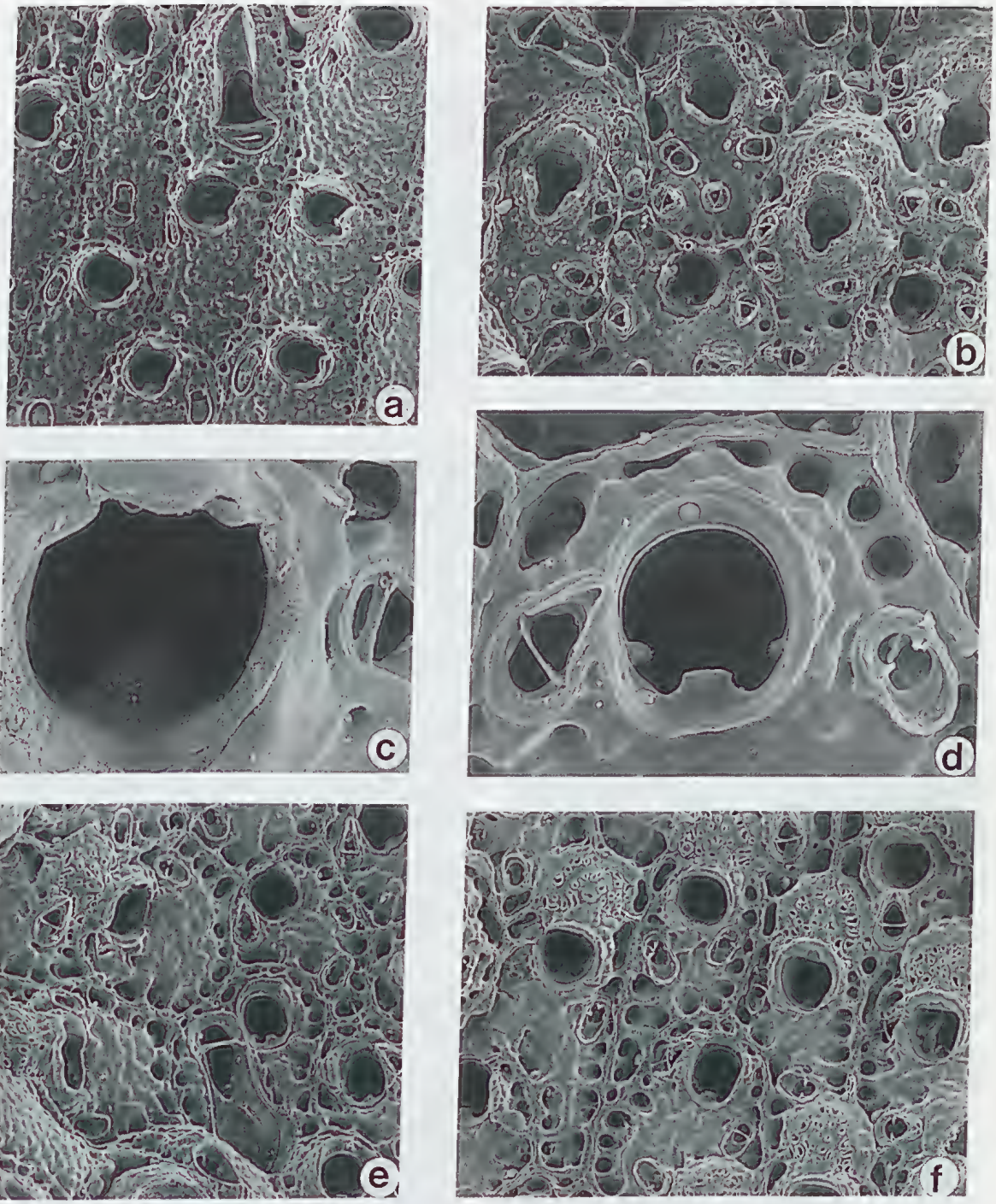


FIG. 21. a-c, *Parasmittina hastingsae*; a, autozooids and a giant avicularium, ×60; b, part of the Hawaiian paratype material, ×55; c, primary orifice, ×250. d-f, *Parasmittina galerita*; d, primary orifice, ×220; e, autozooids and a giant avicularium, ×60; f, ovicelled autozooids, ×55.

edge serrated, distally directed. Ovicell more or less spherical, with 20-30 thickly rimmed, relatively large, frontal pores; the peristome extending onto its frontal surface, forming a complete tube, distal portion of which becoming immersed below an encroaching ooecial cover.

REMARKS

This species was especially abundant in the Heron Island collections. It is distinguished from other species of the genus by the combination of small, oval avicularia (proximally directed when lateral to orifice), and large avicularia with tapered, serrated rostra, which are proximally directed when lateral to the autozooid orifice, but distally directed when interzooidal. *P. hastingsae* was described from Hawaii by Soule & Soule (1973) and subsequently reported from Komodo, Indonesia, by Winston & Heimberg (1986).

Parasmittina galerita sp. nov.
(Fig. 21d-f)

Smittina parsevalii: Harmer, 1957: 941 [part], pl. 65, fig. 5 [only].

TYPE MATERIAL

HOLOTYPE: GH5231, Heron Island, Stn 16, 13 Apr 1972.

ETYMOLOGY

Latin *galerum*, a helmet.

DESCRIPTION

Colony a multilaminar sheet. Autozooids small, rectangular to irregularly polygonal, convex, separated by thickened sutures. Primary orifice about as wide as long; lyrula short, occupying about half total width of orifice; its edge slightly curved; condyles small, rounded, downcurved, with finely denticulate edges; a single, inconspicuous, mid-distal oral spine present in early ontogeny. Peristome widely open proximally, at first consisting simply of paired, subtriangular lateral lappets, extending to enclose the distal border of the orifice in later ontogeny. Frontal wall coarsely nodular, bordered by large, and conspicuous marginal pores. Avicularia frequent, polymorphic: each autozooid typically with two, lateral suboral avicularia, the first short, 0.1mm long, oval or shoe-shaped, proximally directed, the second longer, 0.15mm, with acute triangular rostrum directed disto-medially onto the peristome rim; giant avicularia sporadic, as long as autozooids, the rostrum narrow, spatulate distally, with smooth rim. Ovicell relatively small, wider than long, with about 20 small pores frontally; developing a nodular, peripheral ooecial cover, and a distinct frontal lip where the peristome traverses it.

Measurements (means and standard deviations of 20 values, mm): autozooid length 0.51±0.06; width 0.33±0.04; orifice length 0.10±0.007; width 0.10±0.005.

REMARKS

The specimens assigned to *Cellepora parsevalii* Audouin by Harmer (1957) encompass at least two species. The Red Sea specimen listed by him (Ghardaqa, 4D) is quite distinct from that from Makassar Strait (38I, Siboga Stn 77), which is the same species as that described here from Heron Island. *P. parsevaliformis* Soule & Soule also has just a single mid-distal oral spine, and a similar array of avicularia, with a short oval type proximally directed, and an acute triangular type directed disto-medially onto the peristome. However, *P. parsevaliformis* differs from *P. galerita* in its longer orifice, narrower sinus, with distinctly cusped corners, and in its ovicell, which is smooth frontally, with a peripheral band of relatively large pores.

Parasmittina latiavicularia (Kirkpatrick)
(Fig. 22a-c)

Smittia latiavicularia Kirkpatrick, 1888: 80, pl. 10, fig. 3.

Parasmittina latiavicularia: Hayward, 1988: 301, fig. 5a.

Parasmittina leviavicularia Soule & Soule, 1973: 409, figs 7E-G.

DESCRIPTION

Colony a small, irregular, multilaminar patch. Autozooids oval to hexagonal, convex, separated by distinct sutures; 0.45-0.7×0.35-0.45mm. Primary orifice longer than wide, distinctly oval, the distal border with a few indistinct denticulations medially; lyrula occupying about half width of proximal edge, slender, with curved edges and cusped corners; condyles oval, prominent, downcurved, with finely denticulate edges. One or two slender, distinct oral spines present in early ontogeny. Peristome consisting almost entirely of paired lateral lappets; widely open proximally. Frontal wall nodular, bordered by a single or double series of large pores. Avicularia numerous: characteristically, single or paired lateral oral, with acute triangular rostrum disto-medially directed, ascending the peristomial lappet; either or both replaced by a short, oval or shoe-shaped avicularium, with proximally directed rostrum; in some autozooids the triangular avicularium may be medio-proximally situated, with the rostrum distally directed, along the edge of the peristome; in older parts of the

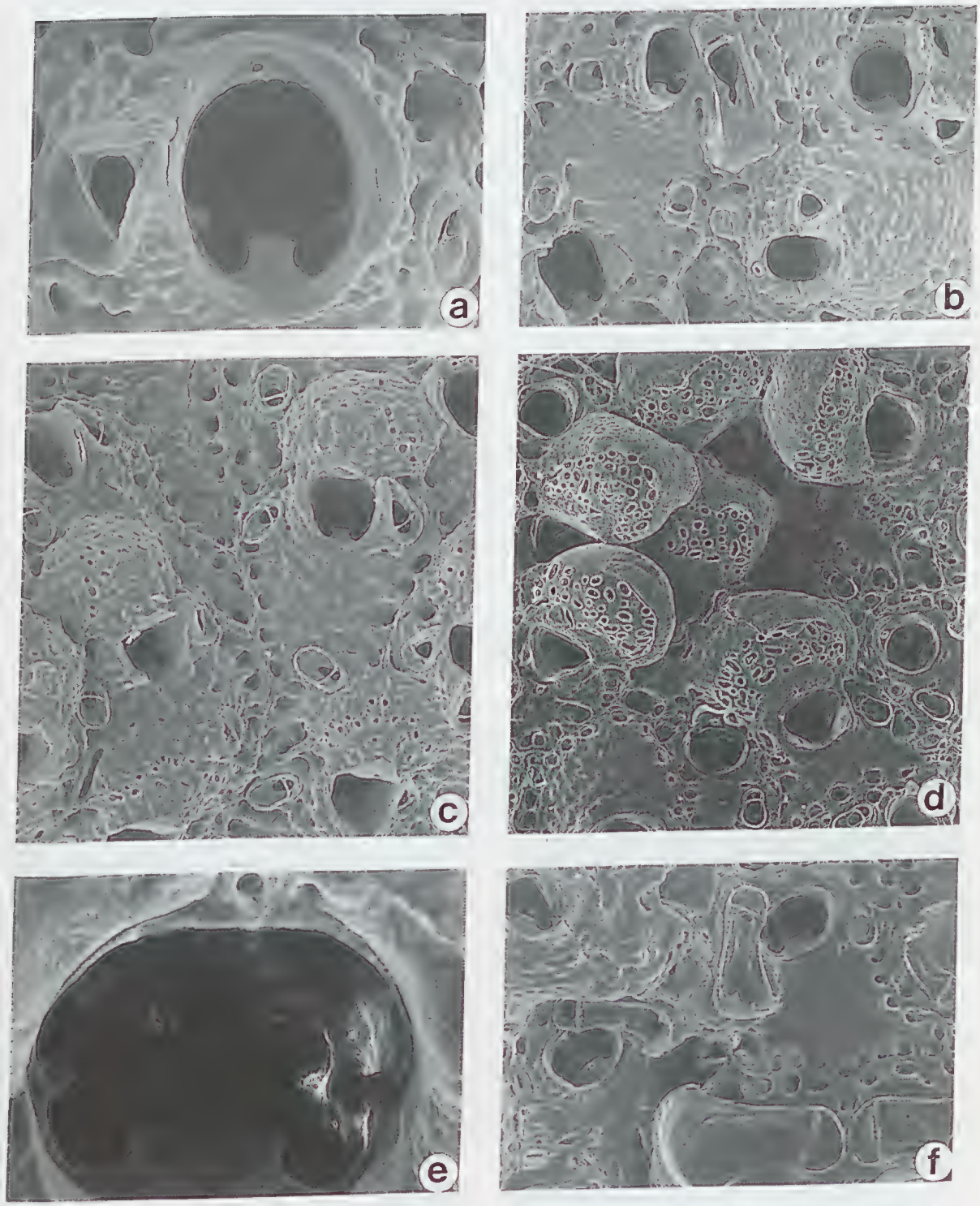


FIG. 22. a-c, *Parasmittina latiavicularia*; a, primary orifice, ×240; b, autozooids and a giant avicularium, ×90; c, ovicelled autozooids, ×80. d-f, *Parasmittina onychorrhyncha*; d, ovicelled autozooids, ×60; e, primary orifice, ×400; f, autozooids and giant avicularia, ×90.

colony the small oval avicularia may proliferate along the margins of the autozooids. Giant avicularia rare, occasionally replacing the lateral suboral avicularium, rostrum shorter than autozooid, broadened or rather angular distally, with an irregularly cusped rim. Ovicell spherical, prominent, with about 20 small frontal pores; becoming coarsely nodular, developing a distinct frontal lip above the secondary orifice, and often with a well developed umbo.

DISTRIBUTION

This rather inconspicuous species has been previously reported only from Mauritius and Hawaii. It was present in two of the Heron Island samples.

Parasmittina onychorrhyncha sp. nov.
(Fig. 22d-f)

TYPE MATERIAL

HOLOTYPE: GH5232, Heron Island, Stn 25, 18 Apr 1972.

ETYMOLOGY

Greek *Onychos*, a claw, and *rhynchos*, a snout.

DESCRIPTION

Colony an irregular, multilaminar sheet. Autozooids rectangular, hexagonal or oval at growing edges, but often irregularly polygonal in frontally budded laminae; convex, separated by distinct sutures. Primary orifice wider than long; lyrula short and broad, with straight edge, occupying about half proximal border; condyles thin, pointed, downcurved; typically with a single, slender, mid-distal oral spine. Peristome widely open proximally, consisting largely of paired, subtriangular lateral lappets. Frontal wall distinctly nodular, bordered by conspicuous marginal pores. Avicularia sporadic, frequent on some parts of colony, rare elsewhere, polymorphic: most often short, shoe-shaped, about 0.1mm long, proximo-lateral to orifice and proximally directed; less often, about 0.2mm long, distal or disto-lateral to orifice, narrowly spatulate or bluntly triangular, directed proximo-laterally; occasionally gigantic, occupying half frontal area of autozooid, the rostrum broadly spatulate, deeply cupped, with a coarsely toothed distal rim. Ovicell globose, prominent, closely perforated frontally by numerous small, irregular pores; developing a granular ooecial cover, often slightly raised and frilled where it borders the perforate frontal region of the ovicell.

Measurements (means and standard deviations of 20 values, mm): autozooid length 0.59±0.05; width 0.33±0.05; orifice length 0.10±0.007; width 0.12±0.006.

REMARKS

P. delicatula (Busk, 1884), described from Hawaii, and *P. fistulata* (Harmer, 1957), from Indonesia, are very similar species which can be separated principally by the morphology of the primary orifice and the occurrence of particular types of avicularia. These features also serve to distinguish both species from *P. onychorrhyncha*.

Parasmittina serrula Soule & Soule
(Fig. 23e,f, 24a)

Parasmittina serrula Soule & Soule, 1973: 386, figs 3D-F.

Parasmittina serrula: Gordon, 1984: 96, pl. 35, figs B, C.

DESCRIPTION

Colony forming small, glistening white patches, rarely more than 5mm in diameter. Autozooids oval to hexagonal, small, convex, separated by deep grooves; 0.3-0.5×c.0.25mm. Primary orifice wider than long, with denticulate distal border; lyrula occupying about half width of proximal border, with slightly curved edge and cusped corners; condyles downcurved, rounded, with very finely denticulate edges. Two to four long, stout distal oral spines; obliterated in brooding autozooids but persisting into late ontogeny in others. Peristome most prominent laterally and proximally, with a well-marked medio-proximal notch, often flanked on each side by a stout, erect process. Frontal wall finely nodular, bordered by large and distinct marginal pores. Lateral suboral avicularia typically paired, equally-sized; the rostrum slender, parallel-sided, rounded at tip, with very fine serrations along its distal edges; characteristically inclined so that the rostrum lies on its side. Giant avicularia occasional, as long as autozooid, with the rostrum slightly flared distally and very coarsely serrated. Ovicell spherical, smooth, with 15-20 regularly dispersed pores; peristome encroaches onto frontal surface of ovicell in later ontogeny, but an ooecial cover does not seem to develop.

DISTRIBUTION

Soule & Soule (1973) found this to be the commonest species of *Parasmittina* on Hawaiian reefs. It was subsequently described and figured

from the Kermadec Islands by Gordon (1984) and from Belize by Winston (1984). It occurred in three of the Heron Island samples but has not previously been reported from Australia.

Parasmittina turbula sp. nov.
(Fig. 23a-d)

TYPE MATERIAL
HOLOTYPE: GH5233, Heron Island, Stn 25, 18 Apr 1972.

ETYMOLOGY
Latin *turba*, disorder.

DESCRIPTION
Colony encrusting, multilaminar, developing an irregular, mamillate form, the later generations of autozooids lacking regular orientation. Autozooids oval to irregular, convex, separated by distinct sutures; frontal wall irregularly nodular, bordered by large marginal pores, with thickened struts between; 0.5×0.3mm. Primary orifice about as wide as long (0.12mm); lyrula occupying about one-third of proximal width, short, rectangular, with a gently curved edge; condyles oval, downcurved, with finely crenulate edges. A single disto-medial spine present; peristome complete, initially with a delicately flared lip, a deep distal embayment accommodating the spine, and a shallow mid-proximal notch flanked by thickened internal ridges. With ontogenetic thickening the peristome becomes deeper, the distal spine is obliterated and the proximal notch accentuated. Avicularia polymorphic, numerous; one or two lateral to the peristome in newly budded autozooids, usually narrow, parallel-sided, from 0.2-0.3mm long, proximally directed, occasionally shorter, triangular and disto-medially directed; additional avicularia develop in later ontogeny, typically clustered around the peristome, and directed towards the orifice; gigantic avicularia present in a few autozooids, laterally situated and proximally directed, with flared, slightly spatulate mandible. Ovicell spherical, with numerous fine perforations, rapidly enveloped by secondary calcification; with a number of small avicularia developing on its frontal surface, directed towards the autozooidal orifice.

REMARKS
The slender, parallel-sided avicularia recall those of *P. areolata* Soule & Soule. *P. turbula* is distinguished from that species by its single, distal oral spine, the morphology of the lyrula and condyles, and by the clusters of medially directed avicularia developed around the peristome in later ontogeny.

Pleurocodonellina Soule & Soule, 1973

Colony encrusting. Autozooid frontal wall with marginal pores only. Primary orifice with strongly developed condyles; proximal border concave, developed as a broad or shallow sinus. Peristome developing in early ontogeny, completely surrounding orifice, its inner edge often thickened medio-proximally and forming a secondary sinus. Distal oral spines present. Avicularia adventitious, dimorphic, typically situated proximo-lateral to orifice. Ovicell with small, scattered pores. Vertical walls with small uniporous septula.

Type species: *Pleurocodonellina lahainae* Soule & Soule, 1973.

Pleurocodonellina signata (Waters)
(Fig. 24b)

Smittia signata Waters, 1889: 17, pl. 3, figs 4-6.
Smittina signata: Harmer, 1957: 928, pl. 63, figs 27-29.
Parasmittina signata: Winston & Heimberg, 1986: 21, figs 51-54.

DESCRIPTION
Colony forming extensive, pinkish brown, unilaminar sheets. Autozooids commonly 0.5×0.3mm, with a finely nodular frontal wall, bordered by a single series of large and conspicuous areolae. Primary orifice wider than long, with broad, flat condyles delimiting a narrow, rounded, proximal sinus; one to three distal oral spines present in early ontogeny. Peristome thin, erect, completely surrounding orifice and obliterating spine bases. Most autozooids with a single avicularium proximo-lateral to orifice; rostrum slender, elongate triangular, proximally directed. Ovicell recumbent on succeeding autozooid, wider than long; frontal surface slightly flattened, with small distal pores.

REMARKS
Cheetham & Sandberg (1964) tentatively assigned this species to *Rimulostoma* Vigneaux, while noting that the published accounts of both the genus (Vigneaux, 1949) and its Miocene type species (Duvergier, 1921) were inadequate for detailed morphological comparisons. Soule & Soule (1973) suggested that *Smittia signata* Waters might be placed in their genus

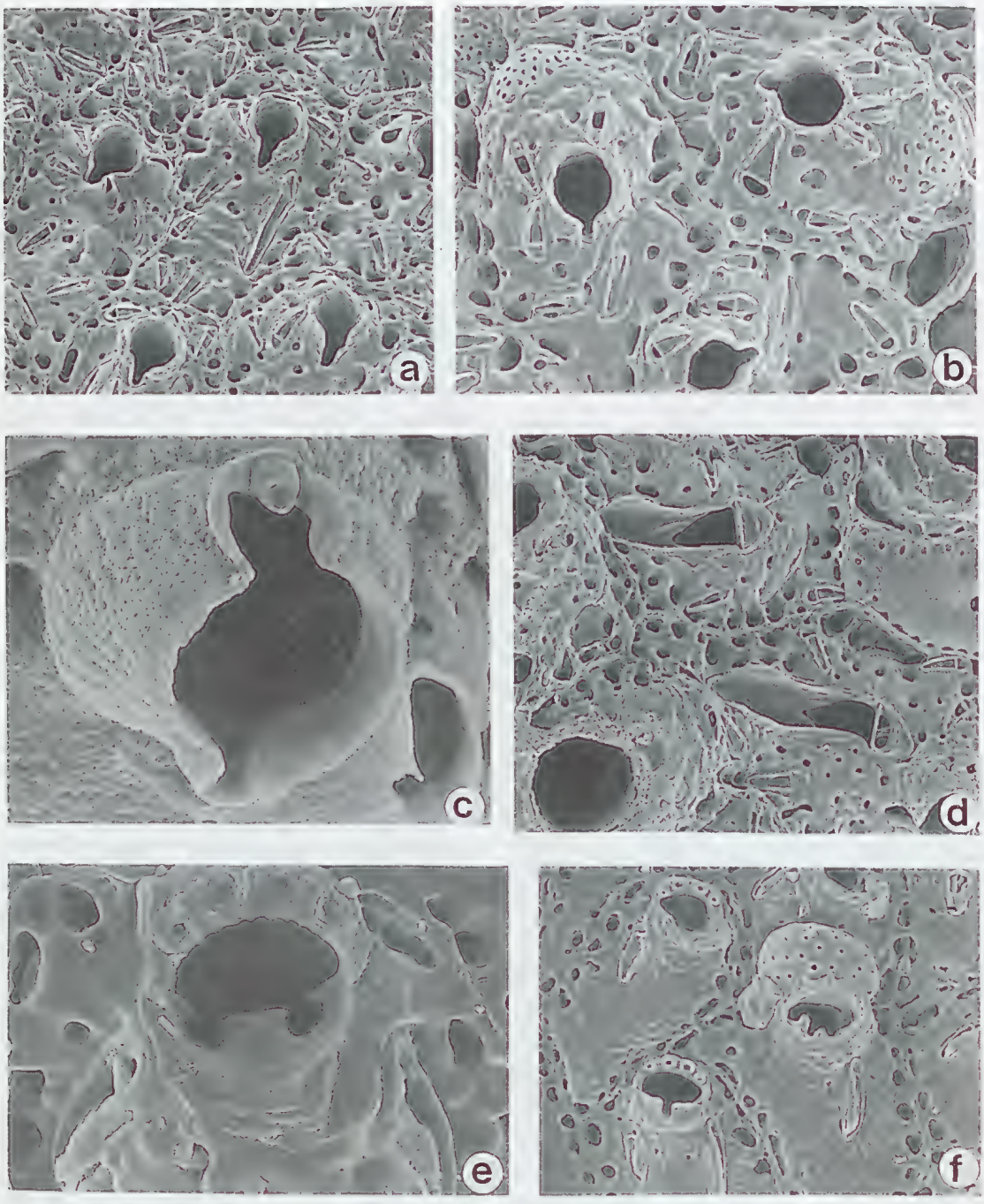
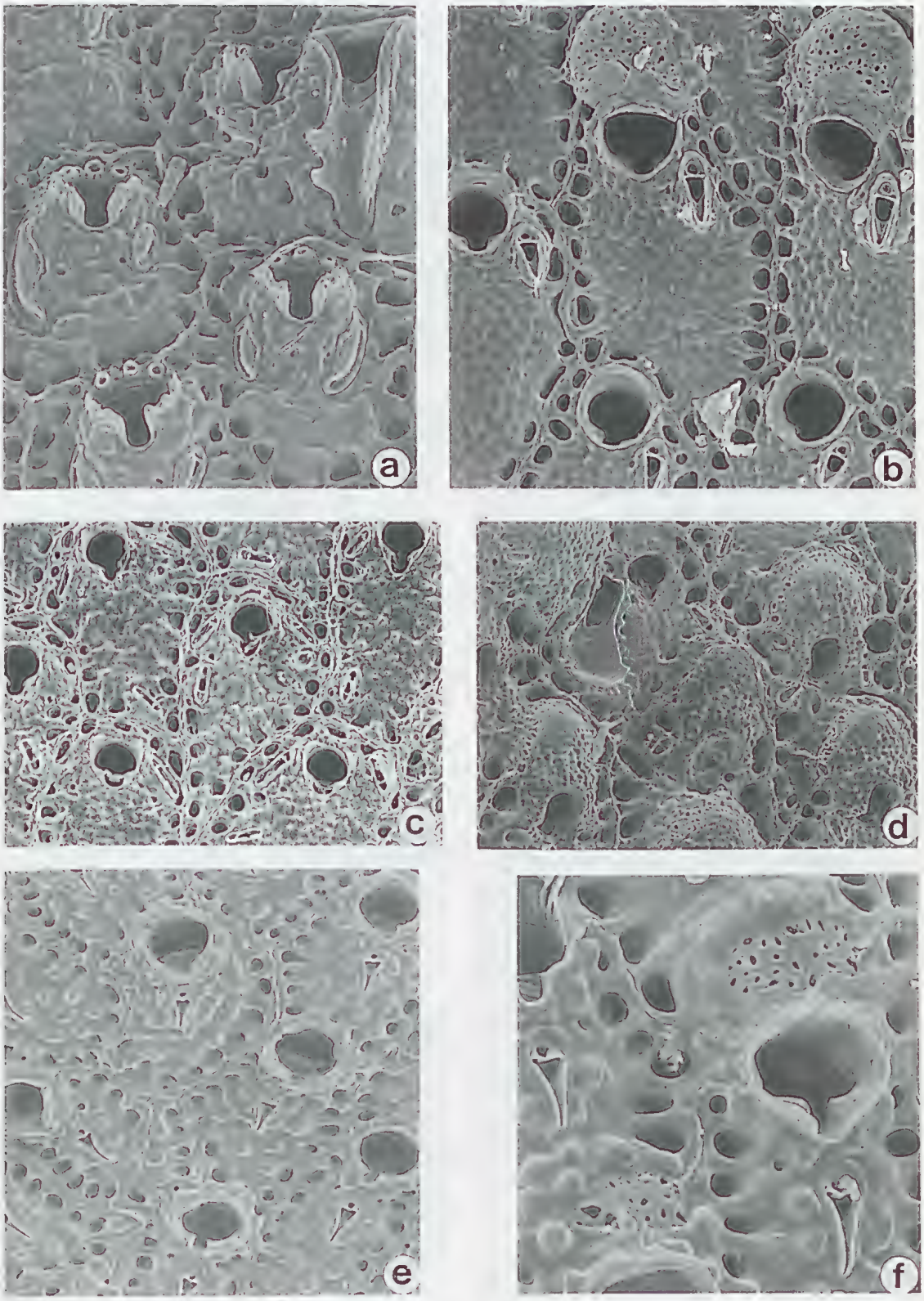


FIG. 23. a-d, *Parasmittina turbula*; a, ×70; b, ×95; c, primary orifice, ×340; d, giant avicularia, ×60. e,f, *Parasmittina serrula*; e, primary orifice, ×350; f, ×80.

FIG. 24. a, *Parasmittina serrula*, ×130. b, *Pleurocodonellina signata*, ×90. c,d, *Pleurocodonellina clavicula*; c, ×60; d, ×60. e,f, *Smittoidea pacifica*; e, ×80; f, ×155.


a
b
c
d
e
f

Pleurocodonellina, and that suggestion is followed here. In all morphological characters *S. signata* conforms to the diagnosis of *Pleurocodonellina*. In particular, the flaring peristomial rim which obliterates the distal spines present in early ontogeny is closely similar to that of the type species, and only a more pronounced development of the paired lateral condyles is necessary to produce the narrow, rounded sinus seen in *P. signata*.

DISTRIBUTION

This species is practically circumtropical in distribution. It ranges throughout the Indo-West-Pacific realm, and has been reported from Mauritius, East Africa, West Africa, and the Caribbean. It is quite common in shallow reef habitats, and at Heron Island occurred in five of the samples studied.

Pleurocodonellina clavicula sp. nov.
(Fig. 24c,d)

TYPE MATERIAL

HOLOTYPE: GH5234, Heron Island, Stn 12, 12 Apr 1972.

ETYMOLOGY

Latin *clavicula*, diminutive of *clavis*, a key.

DESCRIPTION

Colony a broad, encrusting, multilaminar sheet. Autozooids rectangular, hexagonal or irregularly polygonal, rather flat, separated by distinct, thickened sutures. Frontal wall thickly calcified, coarsely nodular, bordered by a single series of large marginal pores. Primary orifice longer than wide, the proximal third comprising a deep, broad, U-shaped sinus, delimited by flat, rounded triangular condyles; encircled by a thin, low, peristomial rim. No oral spines. Avicularia present lateral to orifice in newly budded autozooids, later developed elsewhere along margins of autozooids; slender, parallel-sided, rounded distally and proximally; not infrequently a giant avicularium present, extending down whole length of autozooid, the rostrum 0.4mm long, broadly spoon-shaped, deeply cupped distally, with a coarsely denticulate rim. Ovicell prominent, globular, wider than long, with a crescentic series of irregular pores, developing a coarsely nodular ooecial cover.

Measurements (means and standard deviations of 20 values, mm): autozooid length 0.55±0.05; width 0.37±0.04; orifice length 0.11±0.008; width 0.10±0.01.

REMARKS

The sinuate orifice, encircling peristomial rim, lateral suboral avicularia and perforate ovicell all indicate that this undescribed species is appropriately placed in *Pleurocodonellina*. A single large colony was present in sample 12, from the reef flat west of the cay.

Family PETRALIELLIDAE Harmer, 1957

Colony encrusting; or forming erect, laminate plates. Autozooids with perforated frontal wall. Primary orifice with or without oral spines and condyles. Avicularia adventitious, often associated with orifice. Ovicell with small frontal pores. Vertical and basal walls with multiporous septula.

Sinupetraliella Stach, 1936

Colony encrusting, or erect and bilaminar. Autozooids with regularly perforate, cryptocystidean frontal wall. Primary orifice with asymmetrically developed condyles, defining a small sinus; bordered proximally by a low peristome incorporating a small avicularium. No oral spines. Frontal adventitious avicularia present. Ovicell with entooecium finely perforated, ectooecium largely membranous, developing patches or basal struts of calcification in later ontogeny. Vertical walls with multiporous septula.

Type species: *Petralia litoralis* Livingstone in Hastings, 1932.

Sinupetraliella litoralis (Livingstone in Hastings) (Fig. 25a)

Petralia litoralis Livingstone MS, Hastings, 1932: 438, pl. 1, fig. A, text-fig. 15.

Sinupetraliella litoralis: Harmer, 1957: 706, pl. 45, figs 11-13.

DESCRIPTION

Colony developing broad, loosely encrusting, unilaminar sheets; deep brown in colour. Autozooids rectangular to hexagonal, convex, separated by thin sutures; 0.8-0.9×0.4-0.6mm. Frontal wall thickly calcified, densely perforated by large, round pores. Primary orifice about as wide as long, with a pair of pointed condyles, asymmetrically developed, delimiting an oval,

proximal sinus. Peristome a low rim around proximal and lateral border of orifice, incorporating a small avicularium, 0.1mm long, transversely orientated, its plane perpendicular to orifice, situated immediately above the sinus; in later ontogeny the avicularium partly hidden by a stout mucro developed above it. Frontal adventitious avicularia sparsely developed, usually along margins of autozooids; rostrum slender, elongate oval, variably orientated. Ovicell slightly wider than long, partly overhanging autozooid orifice; entooecium finely perforate, appearing dimpled, ectooecial calcification limited to a narrow, peripheral band and a few radiating struts.

DISTRIBUTION

S. litoralis was described from the Low Isles (Hastings, 1932) and reported by Harmer (1957) from Celebes. Large colonies were present in three of the Heron Island samples.

Family CREPIDACANTHIDAE Levinsen, 1909

Colony encrusting. Frontal wall of autozooids with marginal pores and peripheral spines. Orifice with convex or distinctly rectangular proximal edge, appearing trilobed. Avicularia adventitious, with setiform mandibles. Ovicell hyperstomial, with frontal pores. Vertical walls with small basal pore chambers. Ancestrula tatiform.

Crepidacantha Levinsen, 1909

Colony encrusting, unilaminar. Autozooid frontal wall with marginal pores only; primary orifice contracted laterally, with pronounced lateral condyles, the proximal edge frequently concave, and thus appearing trifoliate; no oral spines. Avicularia adventitious, usually paired, lateral to orifice; mandible setiform. Ovicell hyperstomial, globular, closed by autozooid operculum; with an uncalcified area of ectooecium frontally, bordered by small pores in the entooecium. Small basal pore chambers present, with intervening spinous processes visible in autozooids at the growing margin. Ancestrula tatiform.

Type species: *Flustra poissonii* Audouin, 1826.

Crepidacantha crinispina Levinsen (Fig. 25c)

Crepidacantha poissoni var. *crinispina* Levinsen, 1909: 266, text- figs.1-3, 5, 6.

Crepidacantha crinispina: Brown, 1954: 248, fig. 1C; Gordon, 1984: 100, pl. 37, fig. B.

DESCRIPTION

Colony forming broad, irregular sheets. Autozooids oval to hexagonal, convex, separated by deep grooves; 0.35-0.50×0.25-0.45mm. Frontal wall finely granular, with indistinct marginal pores. Primary orifice longer than wide, with conspicuous lateral processes, appearing distinctly trifoliate. Avicularia paired, situated level with proximal corners of orifice; rostra oval, about 0.05mm long, directed proximally or proximo-medially. Ovicell about as wide as long, entooecium entirely exposed frontally, with only a peripheral band of ectooecium.

DISTRIBUTION

C. crinispina ranges in the western Pacific from New Zealand to the Philippines, and westwards to Indonesia and Thailand. Gordon (1984) reported it as a common intertidal species around North Island, New Zealand. It has also been reported from the southwest Atlantic (Lopez Gappa, 1977) and from Gough Island and Ascension in the central Atlantic (Hayward, 1980).

Crepidacantha carsioseta Winston & Heimberg (Fig. 25d)

Crepidacantha carsioseta Winston & Heimberg, 1986: 27, figs 64-66.

DESCRIPTION

Autozooids oval to hexagonal, 0.35-0.45×0.3mm. Frontal wall smooth, bordered by inconspicuous marginal pores. Primary orifice longer than wide, trifoliate, with a broadly rounded proximal lip. Avicularia paired, proximal to orifice, directed medially; mandible setiform. Ovicell spherical, smooth, with a curved band of pores crossing the frontal surface distally.

DISTRIBUTION

This species has recently been described (Winston & Heimberg, 1986) from two localities in Indonesia and is here reported from Australia for the first time. The material from Heron Island consists of small colonies from sample 25.

Family INVERSIULIDAE Vigneaux, 1949

Colony encrusting. Autozooids with tuberculate frontal wall evenly perforated by small pores;

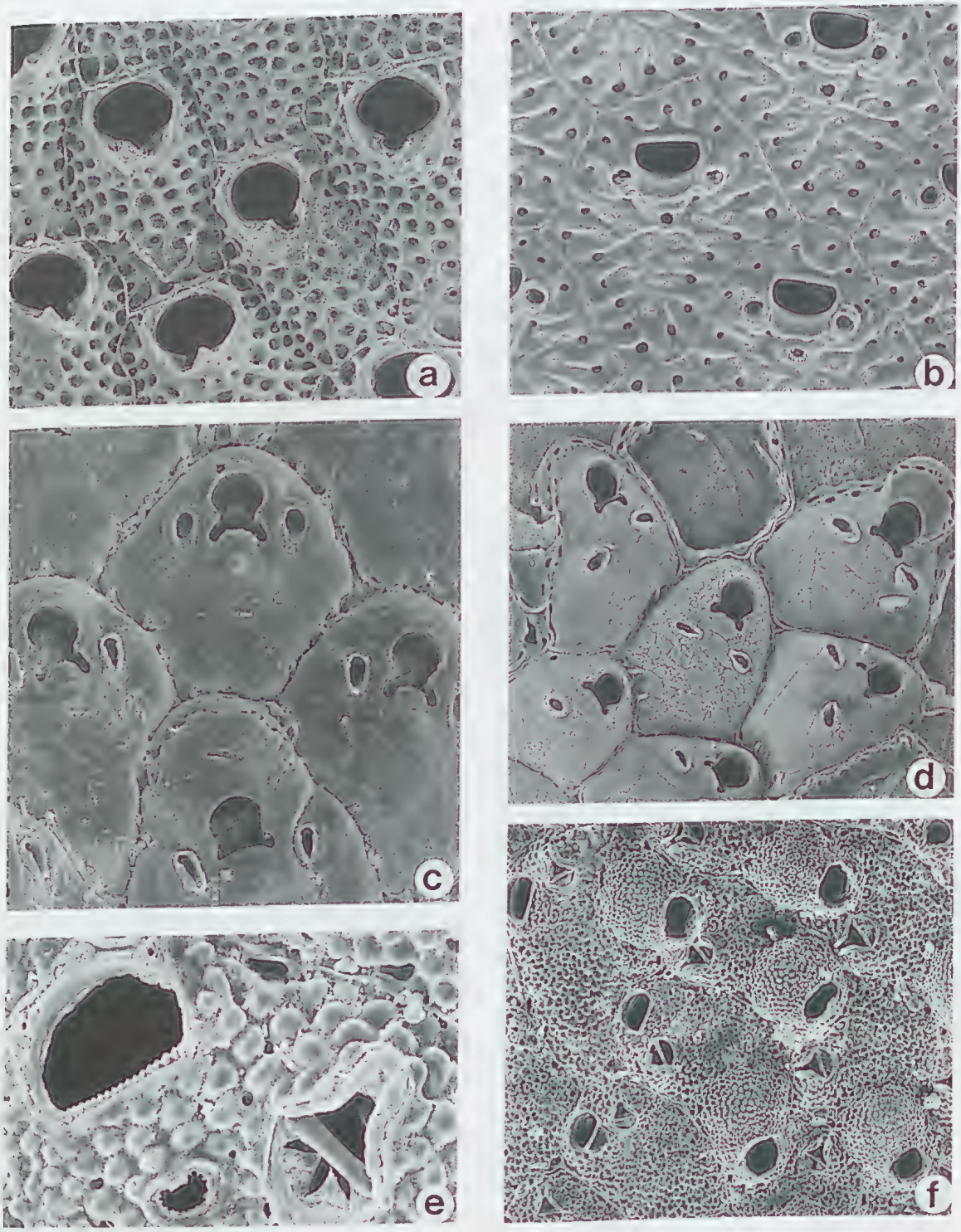


FIG. 25. a, *Sinupetraliella litoralis*, ×40. b, *Inversiula inversa*, ×70. c, *Crepidacantha crinispina*, ×90. d, *Crepidacantha carsioseta*, ×75. e,f, *Microporella orientalis*; e, ×220; f, ×50.

a prominent suboral ascopore present. Orifice with straight distal rim and concave proximal rim, the operculum hinged along its distal edge; no condyles; no oral spines. Avicularia adventitious. No ovicells.

Inversiula Jullien,1888

Colony encrusting, unilaminar. Autozooids with tuberculate frontal wall perforated by numerous simple or stellate pores; primary orifice with reversed orientation, the semicircular operculum hinged along its straight distal edge; ascus opening via a well-defined ascopore proximal to the orifice; no oral spines. Avicularia adventitious; typically paired, lateral to orifice. Embryos brooded internally. Small basal pore chambers present.

Type species: *Inversiula nutrix* Jullien, 1888.

Inversiula inversa (Waters) (Fig. 25b)

Porina? inversa Waters, 1887: 95, pl. 4, fig. 23.
Inversiula inversa: Harmer, 1957: 956, pl. 72, figs 24, 32, 33.

DESCRIPTION

Colony forming small, irregular patches. Autozooids irregularly hexagonal, separated by distinct sutures; 0.55-0.65×c.0.5mm. Frontal wall with raised ridges and tubercles, which form a radiating series around the edges; with distinct marginal pores immersed between thickened ridges, and large, stellate pores over the central part, each on a raised tubercle. Ascopore slightly larger than frontal pores, stellate, also on a thickened tubercle, immediately proximal to orifice. Avicularia proximo-lateral to orifice, paired, shortly columnar; with oval rostrum, 0.06mm long.

DISTRIBUTION

I. inversa has been reported sporadically along the eastern seaboard of Australia, from New South Wales to Torres Strait, and from the Philippine Islands. It was present in two of the Heron Island samples.

Family MICROPORELLIDAE Hincks, 1877

Colony encrusting; or forming erect, bilaminar plates, attached by an encrusting base; or arborescent, freely branching. Autozooid frontal wall evenly perforated, or with marginal pores only; a conspicuous ascopore present proximal to orifice. Orifice typically D-shaped, lacking condyles; oral spines present or absent. Avicularia adventitious, or absent. Ovicell hyperstomial. Vertical walls with basal pore chambers or mural septula.

Microporella Hincks, 1877

Colony encrusting. Autozooids with nodular frontal wall perforated by scattered pores; ascopore situated in distal half of autozooid, conspicuous. Primary orifice D-shaped. Distal oral spines present, but sometimes small, and impermanent. Avicularia adventitious, mandible setiform. Ovicell prominent, imperforate or with few, minute pores; closed by autozooid operculum. Large basal pore chambers present.

Type species: *Eschara ciliata* Pallas, 1766.

Microporella orientalis Harmer (Fig. 25e,f)

Microporella orientalis Harmer, 1957: 962, pl. 62, figs 25-28, 38.
[not] *Microporella orientalis*: Gordon, 1984: 103, pl. 39, fig. C.

DESCRIPTION

Colony developing broad, unilaminar sheets. Autozooids oval to hexagonal, convex, separated by distinct sutures; 0.5-0.7×0.35-0.5mm. Primary orifice wider than long, 0.08× 0.12mm, the proximal edge finely denticulate. Three slender, distal oral spines present in early ontogeny, missing in most autozooids distant from growing edge. Frontal wall appearing distinctly nodular, densely perforated by small, round pores. Ascopore separated from proximal edge of orifice by a distance slightly less than one orifice length, with slightly thickened rim and coarsely denticulate, crescentic lumen. A single avicularium on each autozooid, situated lateral to ascopore, with broad, thick crossbar and semicircular proximal opesia; the rostrum abruptly tapered and narrowest distally; mandible heavily sclerotized and appearing dark brown, 0.2-0.25mm long, setiform, or variously broadened on one or both sides of the median rachis, and typically with a pair of short, hooked, lateral processes close to the base. Ovicell more or less spherical, nodular, with minute pores scattered over its surface; brooding autozooids develop a thickened peristomial rim, peaked medially, which passes distal to the ascopore and fuses on each side with the ovicell.

REMARKS

Harmer (1957) possibly included more than one species in his account of *M. orientalis*, and his synonymy needs to be carefully re-examined. The Heron Island specimens have been compared with the holotype (Siboga Stn 50, W. Flores), and found to be almost identical to it; the size and shape of the primary orifice are characteristic for the species, as are the three delicate, distal oral spines. The avicularian mandible varies in form throughout a single colony and there is no utility in denoting those specimens with lanceolate mandibles as '*orientalis* var.' (Harmer, 1957:963). It is probable that *M. orientalis* occurs generally throughout the western Pacific, and perhaps extends into the Indian Ocean, but the wider geographical distribution accorded it by Harmer (1957) should not be accepted until all of the specimens and records listed by him have been scrutinized again. The *M. orientalis* described and figured by Gordon (1984) has four to six oral spines, a smooth proximal border to the orifice, an incomplete peristome in brooding autozooids, and a striking, saucer-like rim to the ascopore; it clearly represents a distinctly different species.

Microporella fimbriata sp. nov.
(Fig. 26a-c)

TYPE MATERIAL

HOLOTYPE: GH5235, Heron Island, Stn 25, 18 Apr 1972.

PARATYPE: GH5236, as for holotype.

ETYMOLOGY

Latin *fimbria*, a fringe.

DESCRIPTION

Colony forming an extensive unilaminar sheet. Autozooids oval to hexagonal, broad and rather flat, separated by distinct sutures; 0.5-0.65× 0.5-0.6mm. Primary orifice wider than long, proximal edge with a slightly curved, coarsely denticulate inner rim, the outer tooth on each side especially prominent. Four slender distal oral spines present in the youngest autozooids, lost in later ontogeny. Frontal wall coarsely nodular, densely perforated by regularly distributed, round pores; ascopore close to orifice, separated from its proximal edge by a distance equivalent only to one-third of orifice length; rim oval, thickened, smooth, lumen shallowly crescentic, with fine denticulations. Each autozooid with a single avicularium lateral to ascopore, without a pronounced rostrum, but with its frontal surface symmetrical about a pair of stout, median condyles; mandible thin, setiform, up to 0.7mm long, laterally directed when at rest. Ovicell comparatively small, slightly wider than long, coarsely nodular, with scattered, minute pores; aperture rather angular, with a smooth, thickened border.

REMARKS

This is possibly the species described from Sumbawa, Indonesia by Harmer (1957), who referred it to the North Pacific species *M. vibraculifera* Hincks.

Fenestrulina Jullien, 1888

Colony encrusting, unilaminar. Frontal wall of autozooid with pores in marginal series, or scattered over its entire surface; pores typically stellate or complexly reticulate; ascus opening via a conspicuous ascopore proximal to primary orifice, often denticulate or reticulate. Primary orifice D-shaped, with straight proximal edge; spines present or absent. Avicularia absent. Ovicell with membranous ectooecium, calcified entooecium, and marginal pores. Large basal pore chambers present.

Type species: *Cellepora malusii* Audouin, 1826.

Fenestrulina caseola Hayward
(Fig. 26d)

Fenestrulina caseola Hayward, 1988: 325, pl. 10, fig. d.

DESCRIPTION

Colony forming flat, unilaminar sheets. Autozooids oval to irregularly hexagonal, broad, gently convex; commonly 0.6×0.5mm. Frontal wall densely perforated by large, round, stellate pores; ascopore separated from proximal edge of orifice by a distance equivalent to orifice length, with crescentic, denticulate foramen. No oral spines. Ovicell broader than long, depressed and not very prominent; frontal surface with a thickened transverse ridge; marginal pores small, indistinct.

DISTRIBUTION

A single large colony was present in sample 25. This species was recently described from the Mascarene Islands, Indian Ocean (Hayward, 1988), and the Heron Island record thus marks only its second reported occurrence.

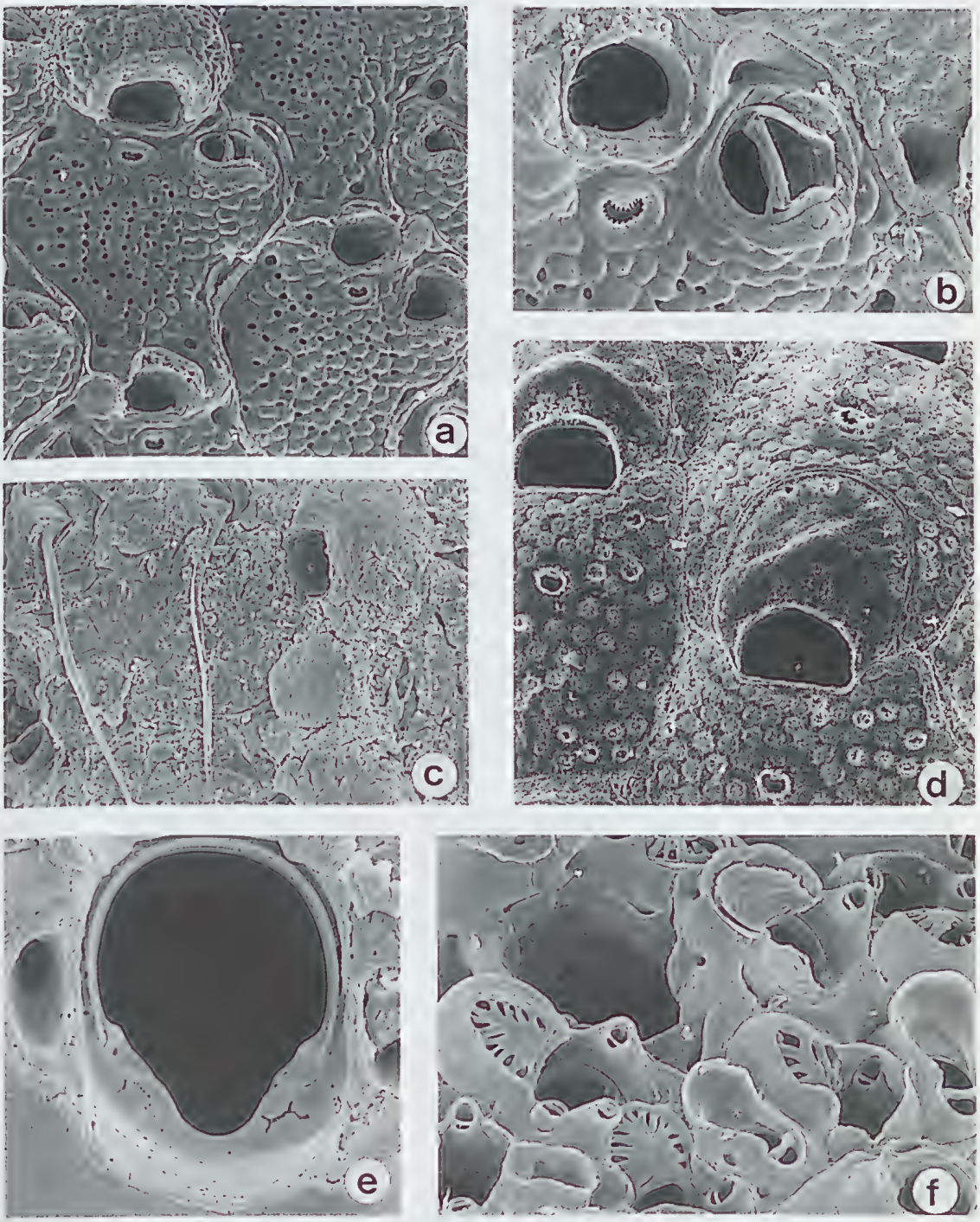


FIG. 26. a-c, *Microporella fimbriata*; a, ×80; b, ×170; c, uncleaned autozooids, to show avicularian mandibles, ×80. d, *Fenestrulina caseola*, ×90. e,f, *Celleporina reginae*; e, primary orifice, ×330; f, ×110.

Family MARGARETTIDAE Harmer, 1957

Colony erect, branching, jointed, attached by cuticular rhizoids. Autozooids with ridged frontal wall, perforated by minute pores, with a median ascopore. Primary orifice rounded, hidden by a projecting, tubular peristome. No spines. No avicularia. Ovicell submerged in peristome, which is conspicuously inflated in brooding autozooids. Ancestrula erect, resembling later autozooids, with a chitinous basal attachment.

Margaretta Gray, 1843

Colony erect, branching, jointed, attached by cuticular rhizoids; consisting of cylindrical, straight or curving, internodes linked by brown cuticular nodes, each arising from a short, calcified basis rami developed by the parent internode. Each node and basis rami consists of single, double or triple tubes. Autozooids ordered in whorls of two to eight around the axis of the internode; frontal wall granular, densely perforated and appearing reticulate; a disto-medial ascopore present. Primary orifice orbicular, visible only in earliest ontogeny, obscured by a long, cylindrical peristome, typically perforated and longitudinally ridged. No spines. No avicularia. Ovicell peristomial, hidden; brooding autozooids with dimorphic peristomes, typically longer, curved, or with a modified secondary orifice.

Type species: *Cellaria cereoides* Ellis & Solander, 1786.

Margaretta tenuis Harmer
(Fig. 27a)

Margaretta tenuis Harmer, 1957: 840, pl. 55, figs 13-18.

Margaretta tenuis: Hayward, 1988: 330, pl. 11, fig. a.

DESCRIPTION

Colony generally sparsely branched, internodes 2-3mm long, 0.5mm wide. Autozooids in triple whorls, 0.8-1.0×c.0.4mm, fusiform, with finely and regularly reticulate frontal shields, the boundaries between adjacent autozooids not distinct. Basis rami tripartite; nodes consisting of short, tripartite tubes. Peristomes of fertile autozooids projecting at right angles to internode axis, but otherwise not markedly different from others.

DISTRIBUTION

M. tenuis has been reported from Queensland, Torres Strait, the Philippine Islands, and from many Indonesian localities; it ranges westwards to Mauritius and the Red Sea.

Margaretta triplex Harmer
(Fig. 27b)

Margaretta triplex Harmer, 1957: 841, pl. 55, figs 8-11.

Margaretta triplex: Ryland, 1984: 72, fig. 39.24; Winston & Heimberg, 1986: 30, figs 70-72.

DESCRIPTION

Colony stout, richly branched, up to 100mm high; internodes straight or curved up to 30mm long, 1mm wide. Autozooids in whorls of four, 1.2-1.4×c.0.6mm, elongate oval, the frontal walls finely reticulate, boundaries between autozooids generally distinct. Basis rami and node tripartite. Peristomes of fertile autozooids projecting at right angle to internode axis, short, very broad based and appearing volcano-like in profile.

DISTRIBUTION

M. triplex is known from Queensland, Torres Strait and Indonesia, and has also been reported from Zanzibar.

Superfamily CELLEPOROIDEA Johnston, 1838
Family CELLEPORIDAE Johnston, 1838

Colony encrusting, multilaminar, pisiform, nodular or mamillate; or erect, attached by an encrusting base, irregularly lobed or branched. Autozooids without regular orientation; frontal wall smooth, with marginal pores. Orifice with concave or conspicuously sinuate proximal border; condyles present; spines present or absent. Avicularia adventitious, and/or vicarious or interzooidal; frequently polymorphic. Ovicell present, variously perforated, not closed by autozooid operculum.

Turbicellepora Ryland, 1963

Colony encrusting, multilaminar, often nodular or massive, or erect and branching. Frontal wall of autozooid with marginal pores only. Primary orifice with sinus; oral spines present or absent. Avicularia polymorphic: adventitious, lateral-oral; vicarious, varying in size. Ovicell with scat-

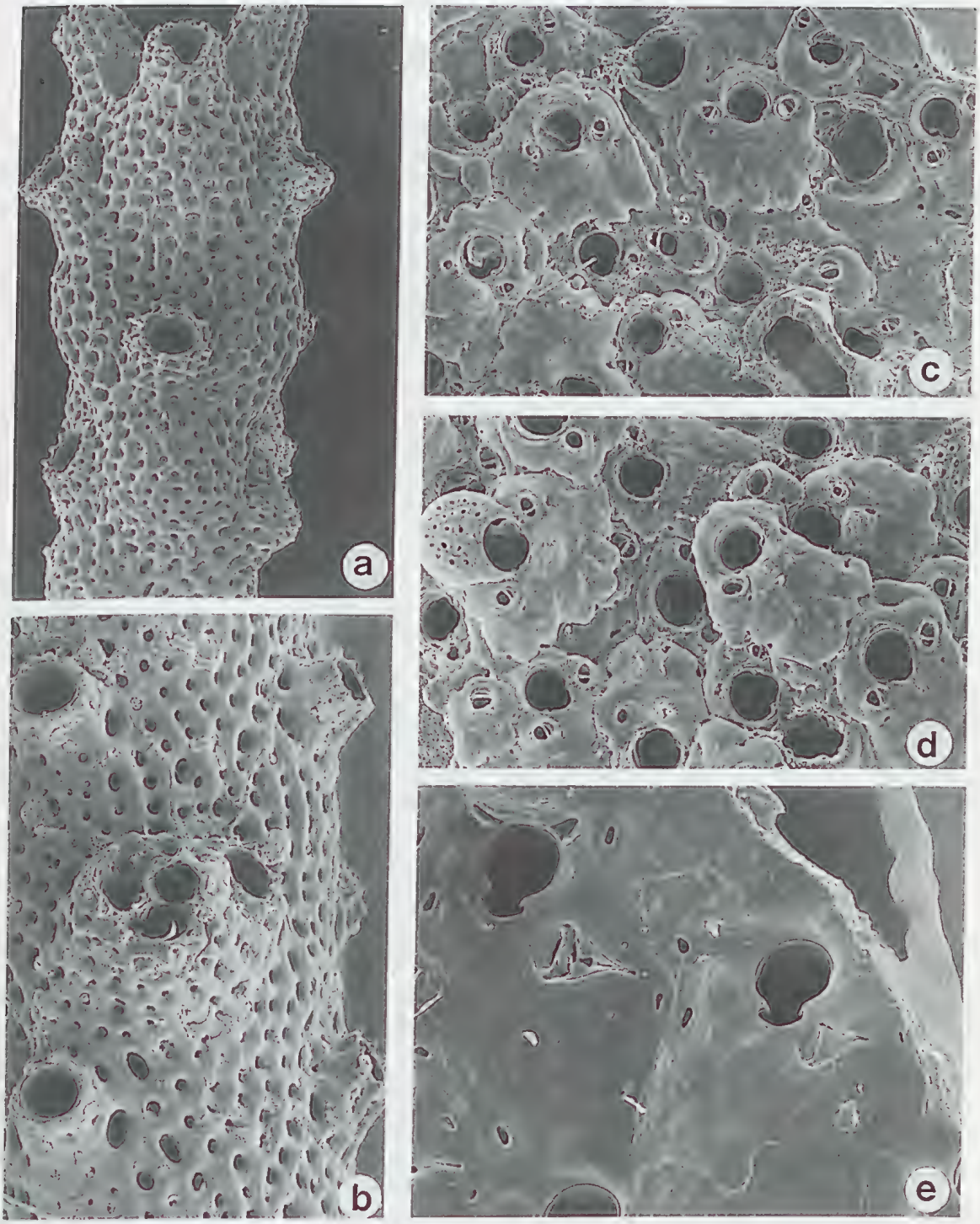


FIG. 27. a, *Margaretta tenuis*, branch tip, ×50. b, *Margaretta triplex*, part of a branch showing a triple branch base, ×50. c,d, *Turbicellepora ampla*; c, ×50; d, ×55. e, *Schedocleidochasma porcellanum*, ×90.

tered frontal pores, not closed by autozooid operculum. Basal pore chambers present.

Type species: *Cellepora coronopus* Wood, 1844.

Turbicellepora ampla (Kirkpatrick) (Fig. 27c,d)

Schizoporella ampla Kirkpatrick, 1888: 76, pl. 7, fig. 4.

Stephanosella bernardii: Harmer, 1957: 1051, pl. 74, figs 21-23.

Turbicellepora ampla: Hayward, 1988: 341, figs 6d,e.

DESCRIPTION

Colony forming multilaminar, nodular encrustations. Autozooids strongly convex, with distinct, lobed, boundaries; the frontal wall smoothly calcified, with indistinct, radiating folds; marginal pores small and inconspicuous. Primary orifice 0.12mm long, with a broad, V-shaped sinus comprising about one-third its length; with a pronounced distal and lateral peristomial rim; no oral spines. Lateral oral avicularia single or paired; rostrum oval, acute to frontal plane, disto-laterally directed. Vicarious avicularia dimorphic: with oval rostrum similar to, but larger than, the lateral oral type, or larger with broadly spatulate rostrum. Ovicell with numerous small, papillate frontal pores.

DISTRIBUTION

This species was originally described from Mauritius (Kirkpatrick, 1888). It is known from a number of localities in the Indo-Malayan region, but its presence in the Red Sea has yet to be substantiated (Hayward, 1988).

Celleporina Gray, 1848

Colony encrusting, pisiform or lenticular, multilaminar. Orifice with a sinus; flanked by paired lateral oral avicularia, with columnar chambers, incorporated into the peristome. Ovicell prominent, spherical, with a perforated area of entooecium, the tabula, frontally; not closed by the zooidal operculum. Small basal pore chambers present.

Type species: *Lepralia hassallii* Johnston, 1847.

Celleporina reginae sp. nov. (Fig. 26e,f)

TYPE MATERIAL

HOLOTYPE: GH5237, Heron Island, Stn 16, 13 Apr 1972.

ETYMOLOGY

Latin *regina*, queen.

DESCRIPTION

Colony encrusting, mamillate. Autozooids at growing edge convex; 0.4-0.45×0.25-0.35mm; frontal wall smooth, with few, relatively large marginal pores. Primary orifice longer than wide, with a broad, U-shaped sinus comprising more than one-third its total length; condyles thickened and rounded; no oral spines. Paired lateral oral avicularia present, with slender, columnar cystids; rostra elliptical, with finely dentate distal edges, acute to plane of orifice and invariably directed laterally. A low, thin peristome encloses the proximal half of the orifice, between the two avicularia, but does not obscure it. Vicarious avicularia frequent, up to 0.25mm long, the rostrum broadly spatulate and deeply cupped distally; crossbar stout, lacking a columella. Ovicell slightly longer than wide; ectooecium thick and smooth, with a thickened ridge bordering the frontal area of entooecium; frontal marginal pores large, elongate and slit-like, so that the entooecium appears to consist of a radiating series of fused struts.

Measurements (means and standard deviations of 20 values, mm): orifice length 0.11±0.007; width 0.10±0.007.

REMARKS

C. reginae is distinguished from other western Pacific species of *Celleporina* by its deeply sinuate orifice, and laterally directed lateral oral avicularia. A single large colony was present in sample 16, from the reef crest northeast of the cay.

Family PHIDOLOPORIDAE Gabb & Horn, 1862

Colony encrusting, unilaminar or multilaminar, often massive; or erect, attached by an encrusting base, forming bilaminar plates, or dichotomously branching arborescent forms, or complex, anastomosed, reticulate structures. Autozooid frontal wall with marginal pores only. Primary orifice with concave or conspicuously sinuate proximal border, the distal border finely denticulate; condyles present; oral spines present or absent. Avicularia adventitious, and/or vicarious or interzooidal. Ovicells present, with uncalcified area of ectooecium frontally; often with a well developed

labellum; median longitudinal fissures characteristic of some genera; not closed by autozooid operculum.

Reteporella Busk, 1884

Colony erect, attached by an encrusting base; branching dichotomously, developing an open arborescent structure, or with the branches anastomosing to form regular reticulate structures; fan-shaped, or cup-shaped, or complexly folded. Autozooids in two to many longitudinal series, on a defined frontal surface; abfrontal surface of colony consisting of blind kenozooids, usually bearing adventitious avicularia. Primary orifice with denticulate distal border, frequently obscured by a sinuate peristome. Avicularia adventitious, polymorphic. Ovicell with a median longitudinal fissure, variably developed.

Type species: *Reteporella flabellata* Busk, 1884.

Reteporella graeffei (Kirchenpauer) (Figs 28c,d, 29a)

Retihornera graeffei Kirchenpauer, 1869: 30.
Reteporella graeffei: Harmer, 1934: 573, pl. 35, figs 12-15; pl. 38, figs 13-15; text-figs 25E, 31, 32; Ryland, 1984: 74, figs 38.11, 40.31-34.

DESCRIPTION

Colony forming an irregular, open or shallowly cupped fan; branches narrow, rather flat, irregularly curved or twisted, dividing dichotomously at irregular intervals, remaining free or anastomosing to leave long, narrow fenestrulae between. Autozooids in four to eight alternating longitudinal rows, flat, or only slightly convex, broadly hexagonal, separated by distinct raised sutures in early ontogeny, but boundaries later rather indistinct. Frontal wall smooth, with two to four proximal marginal pores. Primary orifice wider than long, the proximal border shallowly concave between small, rounded condyles; obscured by a tall proximal peristome, with a longitudinal median fissure, broadened basally to form a labial pore; peristomial rim with two or three short processes proximally, and with one long spine on its inner (i.e., axial) lateral margin, and four on its outer lateral margin. In later ontogeny only a single spine persists on each side. All spines segmented, up 0.3mm long. Avicularia present on frontal walls of autozooids, polymorphic: most frequently 0.1mm long, with semi-elliptical rostrum, and the proximal part produced as a projecting, linguiform process; occasionally larger, with the rostrum acute, and hooked or dentate distally; gigantic avicularia with abruptly hooked rostrum, up to 0.4mm long, present on some marginal autozooids. Ovicell slightly longer than wide, with an elongate median slit. In later ontogeny the proximal regions of the colony are grossly thickened, peristomes become deeply immersed, and additional avicularia are budded.

DISTRIBUTION

R. graeffei is common in shallow reef environments throughout the tropical western Pacific, from Queensland to Japan; it ranges throughout the Indo-Malayan region and westwards to Sri Lanka and East Africa.

Triphyllozoon Canu & Bassler, 1917

Colony erect, fenestrate, attached by an encrusting base. Fan- or cup-shaped, or with the edges complexly folded to form a squat, three-dimensional bun shape. Autozooids opening on one face only of fenestrate sheet, in alternating series along the branches (trabeculae), which anastomose at regular intervals defining oval fenestrulae. Basal surfaces of colony crossed by thickened sutures. Primary orifice with denticulate rim, obscured by a deep peristome with a longitudinal slit (pseudosinus), often partly closed except for a proximal pseudospiramen, typically with a small peristomial avicularium. Oral spines present. Frontal wall with few, large marginal pores. Avicularia adventitious, polymorphic. Ovicell prominent, with a conspicuous, trilobed frontal suture, and a well developed labellum overhanging the aperture.

Type species: *Retepora monilifera* MacGillivray, 1860.

Triphyllozoon mucronatum (Busk) (Fig. 28a,b)

Retepora mucronata Busk, 1854: 120, pl. 26, figs 6a-e.
Triphyllozoon mucronatum: Harmer, 1934: 620, pl. 35, fig. 35; pl. 40, figs 13-20; text-fig. 42.
Triphyllozoon sp.: Ryland, 1984: 74, fig. 40.36.

DESCRIPTION

Colony developing a low bun shape, up to 30mm high with a horizontal spread of up to 60mm, consisting of finely reticulate, deeply lobed folds, anastomosing frequently to form a compact structure. Fenestrulae small, regularly oval, 1.0×0.5mm; trabeculae comprise three to

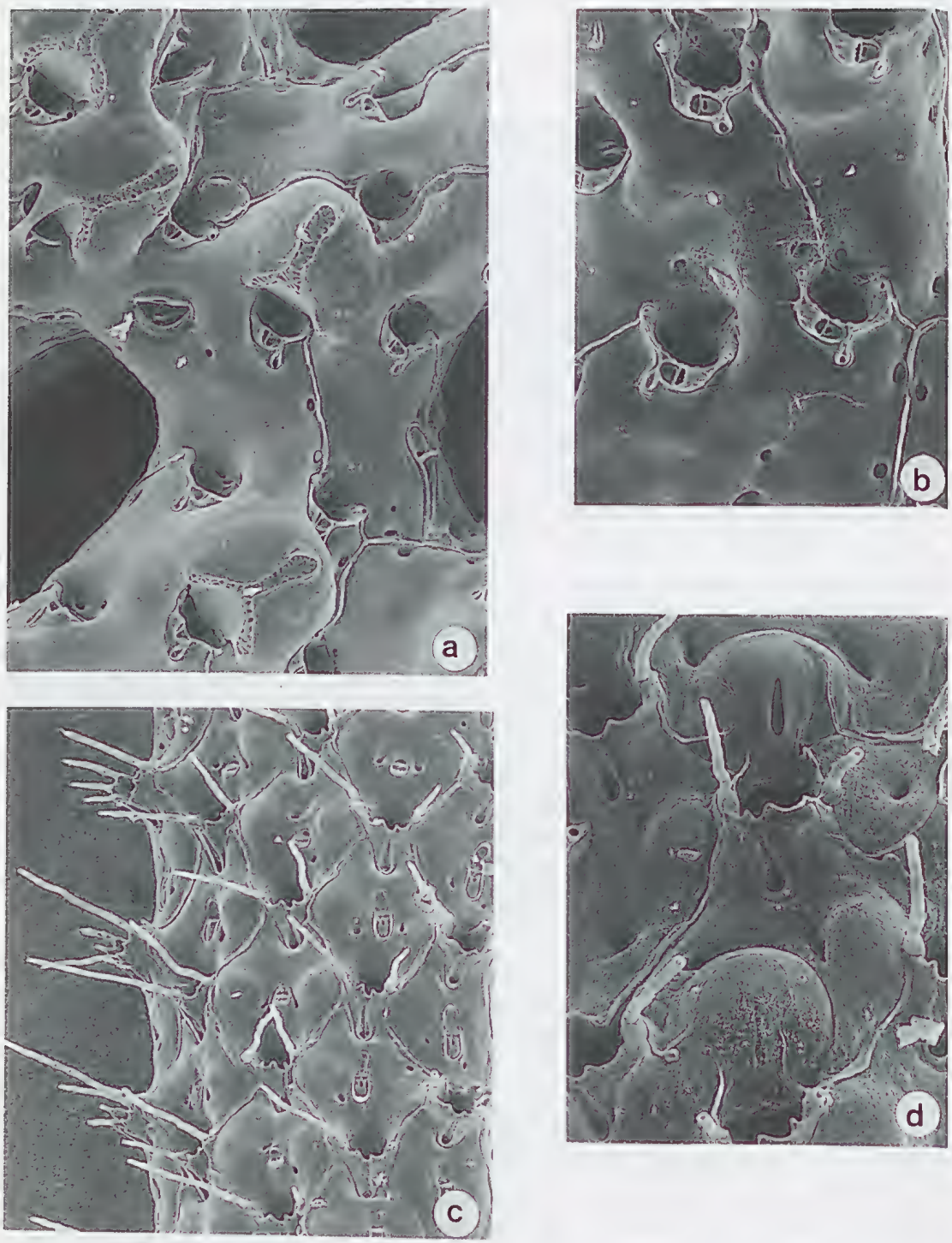


FIG. 28. a,b, *Triphyllozoon mucronatum*; a, ×80; b, ×120. c,d, *Reteporella graeffei*; c, ×60; d, ×130.

five longitudinal autozooid series. Autozooids commonly 0.4×0.2mm, with smooth, convex frontal wall, bordered by a few large, widely spaced marginal pores; sutures between autozooids distinct at growing edge, later progressively obscured. Primary orifice D-shaped, hidden by a deep peristome enclosing its proximal and lateral borders; lip of peristome reflected, with a series of coarse crenulations on its inner edge: medio-proximally a short fissure connects the peristomial rim with the small labial pore, to one side of this is a small peristomial avicularium, acute to frontal plane, laterally directed, with rounded, finely denticulate rostrum. Four short, distal oral spines present in newly budded autozooids, only the proximal pair persisting in later ontogeny. Frontal adventitious avicularia frequent, rostrum 0.1mm long, oval or slightly spatulate. A single large vicarious avicularium present distal or proximal to each fenestrula, with a swollen cystid supporting a narrowly crescentic rostrum; other, larger avicularia occur sporadically, typically within each fenestrula an avicularium with a narrow, elongate rostrum, broadened and denticulate distally; elsewhere, elongate triangular avicularia may be present. Ovicell slightly longer than wide, with a short, square-edged labellum; median frontal fissure longer than proximal fissures.

DISTRIBUTION

This species is known from a few localities in the Philippine Islands, northern New Guinea and eastern Indonesia. It has not been identified previously from Australia.

Schedocleidochasma Soule, Soule & Chaney, 1991

Colony encrusting, uni- or multilaminar. Primary orifice of autozooid cleithridiate (keyhole-shaped), with a deep, arrowhead-shaped or transversely oval sinus below prominent condyles; distal rim of orifice smooth. Oral spines present or absent. Frontal wall with few marginal pores. Avicularia adventitious. Ovicell hyperstomial, partly immersed, not closed by autozooid operculum; with a frontal area of uncalcified ectooecium, and a well-marked labellum. Vertical walls with basal or mural pore chambers.

Type species: *Schedocleidochasma porcellaniforme* Soule, Soule & Chaney, 1991.

Schedocleidochasma porcellanum (Busk) (Fig. 27e)

Lepralia porcellana Busk, 1860: 283, pl. 31, fig. 3.
Cleidochasma porcellanum: Harmer, 1957: 1042, pl. 71, figs 5, 16; Cook 1964b: 11, pl. 1, fig. 4; pl. 2, figs 1, 2; text-figs 4A-E; Winston & Heimberg 1986: 34, figs 85-87.
Schedocleidochasma porcellanum: Soule, Soule & Chaney, 1991: 481.

REMARKS

This familiar species has a circumtropical/subtropical distribution in shallow coastal waters, and may be particularly common in reef flat habitats, on coral rubble, or other hard substrata. At Heron Island it forms flat, silvery, unilaminar sheets, often exceeding 3cm^2. It is readily recognised by the shape of the primary orifice, the lateral suboral avicularium, and its thick, porcellanous secondary calcification. It was present in abundance in seven of the Heron Island samples.

The major revision of *Cleidochasma* by Soule et al. (1991) was published after this paper had been submitted for publication. The specimen illustrated here appears to conform to their concept of *S. porcellanum*, especially in its shallow, transversely oval sinus but, in view of the fact that several previous West Pacific records of this species were shown by Soule et al. to represent their new species, *S. porcellaniforme*, it will be necessary subsequently to review the Heron Island material attributed to *S. porcellanum*.

Rhynchozoon Hincks, 1895

Colony encrusting, multilaminar; discoid, domed, or more usually irregularly spreading, extensive, nodular. Autozooids distinct only at growing edges of colony, or in new, frontally budded laminae; elsewhere immersed to a varying degree in thick secondary calcification. Primary orifice with distal border (anter) beaded or denticulate; proximal border (poster) broadly concave to narrowly sinuate; condyles usually distinct. Oral spines sometimes present in newly budded autozooids. Orifice encircled, and later partly obscured, by marked peristomial thickening, frequently produced into erect or cylindrical, knob-like processes; typically with a distinct notch (pseudosinus) in the proximal border. A transversely or obliquely laterally orientated avicularium located on the proximo-lateral border of the orifice, large and conspicuous, with hooked rostrum and apical process (umbo), or

small and concealed within peristome; often with a stout process (uncinate process) projecting towards the orifice from the inner, proximal edge of the avicularium. Additional, large or small, avicularia present on frontal wall of autozooid, or around peristome rim, often numerous. Frontal calcification of autozooids thick, frequently pearly or distinctly nodular, with marginal pores only. Ovicell typically elongate oval, with a distinct lip (labellum) above the aperture; frontal surface with the outer layer (ectooecium) uncalcified, exposing a smooth or granular area of entooecium (tabula); most often immersed in thickening calcification in early ontogeny and becoming indistinct. Vertical walls with small basal pore chambers.

Type species: *Lepralia bispinosa* Johnston, 1847.

Species of *Rhynchozoon* are common on all tropical reefs and can be particularly difficult to identify. Ontogenetic thickening of the frontal calcification, accompanied by progressive immersion of the primary orifice, and the proliferation of frontally budded avicularia may completely mask those features important for identification. In practice, it is usually impossible to identify any specimen of *Rhynchozoon* without first bleaching a sample to reveal details of the primary orifice. Size and shape of the primary orifice (in particular the sinus), and the morphology of the proximal suboral avicularium are the most important taxonomic features in this genus. In some species, the frontal avicularium and the ovicell provide useful, confirmatory characters.

Rhynchozoon ardeolum sp. nov.
(Fig. 30d,e)

TYPE MATERIAL

HOLOTYPE: GH5238, Heron Island, Stn 25, 18 Apr 1972.

ETYMOLOGY

Latin, diminutive of *ardea*, a heron.

DESCRIPTION

Colony forming broad, multilaminar patches. Autozooids irregularly oval to polygonal, strongly convex, separated by well-marked sutures; commonly 0.45-0.5×0.35-0.4mm. Frontal wall thickly calcified, distinctly corrugated, with a single series of round marginal pores. Primary orifice slightly wider than long, with a short, rounded sinus, bounded by thickened cusps, below blunt, rounded condyles. No oral spines. Many autozooids bearing a very large lateral oral avicularium, with a swollen cystid occupying much of the frontal wall of the autozooid; rostrum broadest proximally, the distal portion, bearing the mandible, elongate, narrow, curved and rounded at the tip, acute to the frontal plane of the autozooid and directed disto-laterally; total length of rostrum 0.3-0.35mm. Additional avicularia sparsely developed, shorter than the lateral oral type, with a narrowly triangular rostrum distal to the mandibular condyles. In later ontogeny frontal calcification thickens, the marginal pores become much accentuated, and three or four stout, conical processes develop around the disto-lateral borders of the orifice, which, however, remains distinct, though partially immersed, and never completely hidden. Ovicells not present.

Measurements (means and standard deviations of 20 values, mm): orifice length (incl. sinus) 0.12±0.004; width 0.12±0.005.

REMARKS

This species is readily distinguished from all other presently known species of *Rhynchozoon* by its unusually large lateral oral avicularium, and by its very distinctive primary orifice. It was present in two of the Heron Island samples.

Rhynchozoon bifurcum Harmer
(Fig. 29b-d)

Rhynchozoon bifurcum Harmer, 1957: 1070, pl. 70, figs 6, 13-15.

DESCRIPTION

Colony a multilaminar, mamillate sheet. Autozooids at growing edge oval, convex, separated by shallow grooves; about 0.5× 0.3mm. Primary orifice wider than long, about 0.16×0.10mm; proximal border shallowly concave between inconspicuous proximo- lateral condyles; no oral spines. Frontal wall nodular, with closely spaced, conspicuous marginal pores. Lateral suboral avicularium present in all autozooids, prominent, with swollen cystid, and broadly triangular, distally hooked rostrum; proximally, a slender subtriangular uncinate process projects above the primary orifice. A stout mucro developing on avicularium, contributing to the peristomial rim, which develops early in ontogeny, obscuring the avicularium and orifice, and eventually consists of six or seven stout, conical processes more or less evenly spaced around the secondary orifice. Frontal

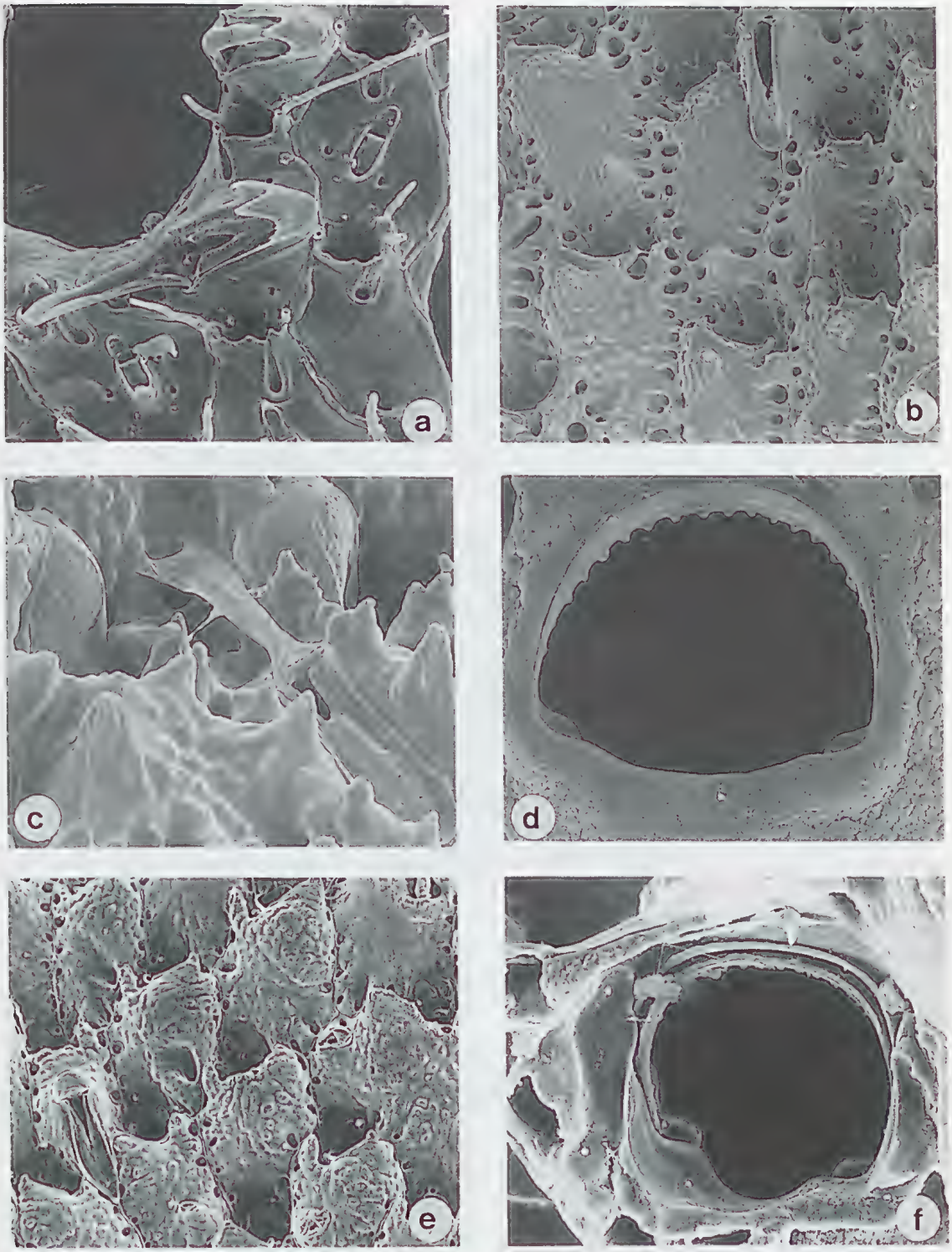


FIG. 29. a, *Reteporella graeffei*, ×90. b-d, *Rhynchozoon bifurcum*; b, ×55; c, an avicularium with bifurcate mandible, ×130; d, primary orifice, ×320. e,f, *Rhynchozoon scopulorum*; e, ×50; f, primary orifice, ×270.

avicularium elongate oval to narrowly spatulate, 0.25-0.5mm long, the mandible in the largest always deeply forked. Ovicell elongate, the frontal surface flat and very finely tuberculate.

DISTRIBUTION

This species is known from Torres Strait, Singapore, and the Chagos Archipelago, but has not been recorded previously from Queensland. The specimen from Japan discussed by Harmer (1957) perhaps does not belong to *R. bifurcum*.

Rhynchozoon compactum (Thornely)
(Fig. 30b,c)

Cellepora compacta Thornely, 1905: 126, pl. fig. 17.
Rhynchozoon compactum: Harmer, 1957: 1076, pl. 70, figs 21-25.

DESCRIPTION

Colony forming irregular, multilaminar patches. Autozooids at growing edge oval to hexagonal, strongly convex, smoothly calcified, about 0.5-0.6×0.35mm. Primary orifice almost circular, about 0.09mm diameter, with a small, U-shaped sinus. No oral spines. A single, lateral-oral, avicularium present in many, but not all, autozooids, the hooked rostrum perpendicular to the plane of the orifice and proximo-laterally orientated. Ovicell as wide as long, the frontal entooecium smooth, labellum indistinctly curved. In later ontogeny the frontal calcification of the autozooid thickens and becomes faintly corrugated; boundaries between autozooids remain distinct, however, and the few small marginal, pores are accentuated. A broad, thick ridge develops around the distal and lateral borders of the primary orifice, characteristically developing two or three knob-like processes, but the orifice remains clearly visible in frontal view. With the development of frontal buds, the primary orifices of the first layer of autozooids become immersed in deep, peristomial tubes, but are not completely hidden. Additional frontal avicularia are sparsely developed, most frequent in later ontogeny; these are up to 0.15mm long, with an elongate oval rostrum.

REMARKS

Heron Island specimens of this distinctive species have been compared with the type material from Sri Lanka, and found to be identical to it. Harmer (1957) listed a specimen from Torres Strait, which it is probably safe to assume belongs to *R. compactum*, but his records from Japan need to be confirmed following re-examination of the specimens listed.

Rhynchozoon haha Hayward
(Figs 30f, 31a,b)

Rhynchozoon haha Hayward, 1988: 334, pl. 11, figs f,g.

DESCRIPTION

Colony developing broad, irregular, spreading sheets. Autozooids at growing edge oval to hexagonal, or rectangular, convex, separated by distinct sutures; 0.5-0.6×0.3-0.35mm. Primary orifice wider than long, with a broad, U-shaped sinus occupying about three-quarters its proximal width; condyles knob-like, small, no oral spines. Frontal wall smooth, with a single series of large, distinct marginal pores. A large, lateral suboral avicularium present on most autozooids; cystid swollen, frequently with a small umbo on its frontal surface; rostrum acute to frontal plane, directed disto-laterally, acuminate but with only a slight distal hook; proximally the avicularian rostrum thickens to form a short, blunt, uncinate process. Frontal adventitious avicularia characteristic: typically one per autozooid, 0.2mm long, directed proximally or proximo-laterally; lozenge-shaped, with the narrowly triangular rostrum about twice as long as the proximal opesia. Ovicell short, smooth frontally, completely immersed by ooecial cover and not readily visible in frontal view. With ontogenetic thickening the primary orifice becomes deeply immersed, hiding the suboral avicularium; four or five stout, conical umbones develop on the peristomial rim, with the proximalmost pair flanking a pronounced proximo-medial notch. The frontal avicularia remain distinct, however, and the autozooid boundaries can be recognised by the deep, conspicuous marginal, pores.

DISTRIBUTION

R. haha was founded on material collected from reef habitats around Mauritius (Hayward, 1988). This is only the second occurrence, but it will probably prove to be generally distributed in the Indo-West-Pacific region, in shallow reef habitats.

Rhynchozoon limatulum sp. nov.
(Fig. 31c-e)

TYPE MATERIAL

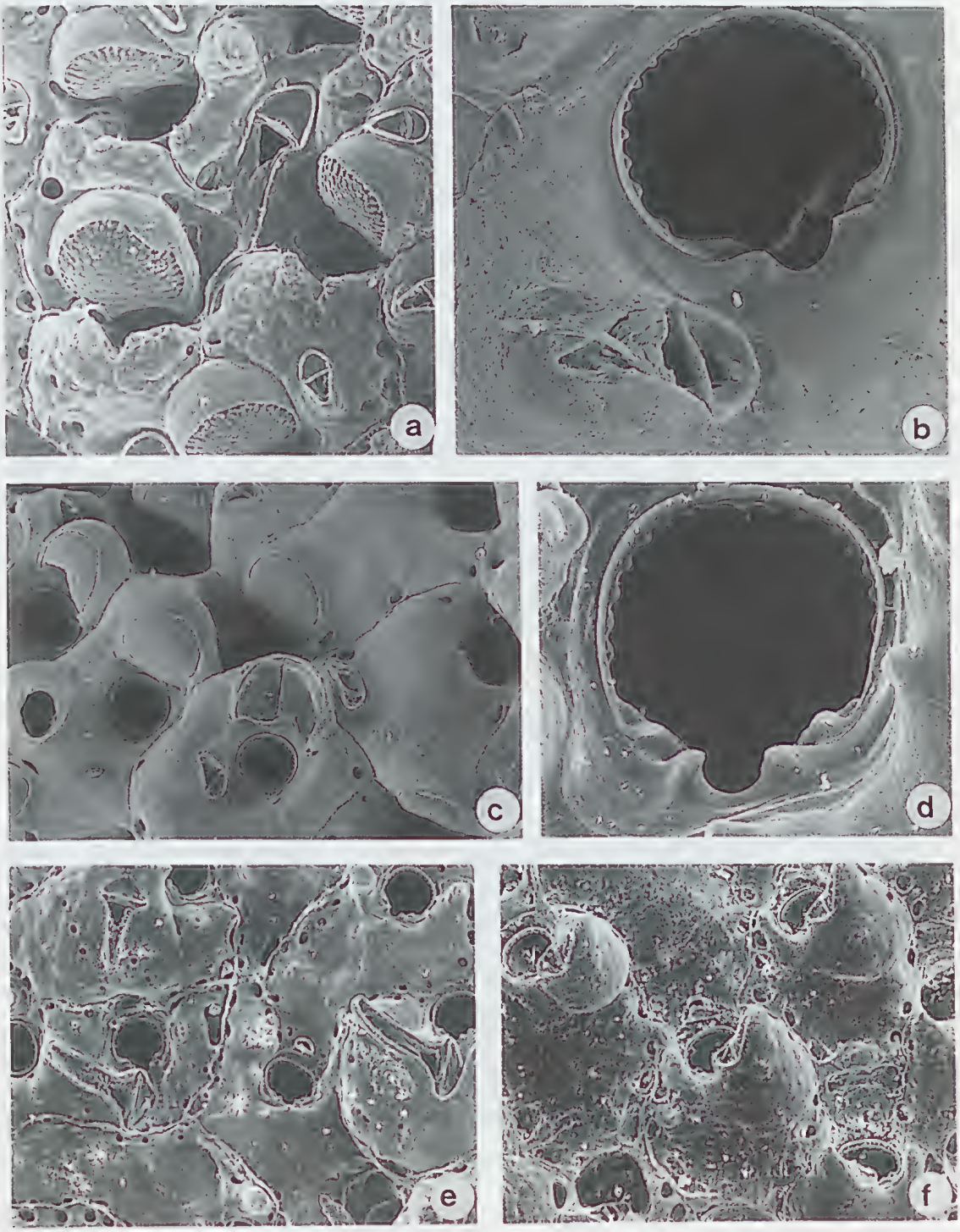


FIG. 30. a, *Rhynchozoon scopulorum*, ×70. b,c, *Rhynchozoon compactum*; b, ×350; c, ×80. d,e, *Rhynchozoon ardeolum*; d, ×350; e, ×60. f, *Rhynchozoon haha*, ×70.

HOLOTYPE: GH5239, Heron Island, Stn 14, 12 Apr 1972.

ETYMOLOGY
Latin, diminutive of *limatus*, polished.

DESCRIPTION
Colony forming irregular, multilaminar sheets. Autozooids at growing edge broadly oval, convex, separated by distinct sutures. Primary orifice distinctly wider than long, with a deep, U-shaped sinus occupying most of proximal width; condyles thickened, conspicuous. No oral spines. Frontal wall smoothly calcified, bordered by small, widely-spaced marginal pores; typically developing two or three prominent, conical processes proximally, forming part of the peristome of the preceding autozooid. Peristome spinous, typically with a single medio-proximal process, paired lateral processes, and two or three distal processes, all prominent, tapered, and occasionally bifurcate apically. Most autozooids with a lateral oral avicularium enclosed within the peristome, the rostrum slender, triangular, hooked distally, and laterally directed. One to three smaller avicularia present on frontal wall; rostrum slender, triangular, laterally directed. Ovicell with a very short labellum and a conspicuous frontal fenestra; rapidly immersed in a smooth ooecial cover.

Measurements (means and standard deviations of 20 values, mm): autozooid length 0.41± 0.04; width 0.30±0.04; orifice length 0.08±0.004; width 0.10±0.003.

REMARKS
This species is distinguished from others in the Heron Island reef flat fauna by its short, wide primary orifice, and comparatively deep sinus. The smooth frontal calcification, spinous peristomes and small frontal avicularia are also characteristic.

Rhynchozoon scopulorum sp. nov.
(Figs 29e,f,30a)

TYPE MATERIAL
HOLOTYPE: GH5240, Heron Island, Stn 16, 13 Apr 1972.

ETYMOLOGY
Latin *scopulosus*, rocky.

DESCRIPTION
Colony forming broad, spreading sheets. Autozooids at growing edge oval to hexagonal, convex, separated by distinct sutures. Primary orifice about as wide as long, with shallow, U-shaped sinus occupying about half proximal width; condyles rounded, distinct; distal and disto-lateral denticulations fine, closely spaced. No oral spines. Frontal wall distinctly nodular, with few, widely spaced, marginal pores. Lateral suboral avicularium large and prominent; rostrum acute to frontal plane, laterally directed, hooked distally; proximally, the rostral rim is produced as a stout, conspicuous uncinate process, almost reaching the opposite side of the peristome, delimiting a rounded pseudosinus. A small adventitious avicularium present on the frontal wall of most autozooids, the rostrum triangular, acute to frontal plane, usually directed proximally. Large frontal avicularia sporadic: 0.4mm long, occupying most of autozooid frontal wall, proximally directed; rostrum lanceolate, often asymmetrical, with upturned tip. Ovicell longer than broad, projecting well above peristomial rim and remaining distinct in later ontogeny; frontal surface slightly flattened, minutely tuberculate. In later ontogeny the suboral avicularium becomes submerged within the peristome, and the proximal peristomial rim bears a pair of short, conical umbones, with a shallow, U-shaped notch between.

Measurements (means and standard deviations, mm)): autozooid length (n = 20) 0.56±0.05; width 0.33± 0.03; orifice length (n = 10) 0.11± 0.005; width 0.14± 0.000.

REMARKS
This species is similar to the Indonesian *R. detectum* Harmer, 1957, recently described and figured by Winston & Heimberg (1986). However, *R. detectum* is distinguished from *R. scopulorum* by its primary orifice, which is only very shallowly concave proximally, and by its large frontal avicularia, which are narrower and more distinctly pointed than in *R. scopulorum*. The large avicularia of the latter are in fact almost identical to those of *R. triangulare* Harmer, 1957, also described from Indonesia; the primary orifice of *R. triangulare*, however, has a slit-like proximal sinus. *Rhynchozoon scopulorum* seems to be common at Heron Island; large colonies were present in six of the samples studied.

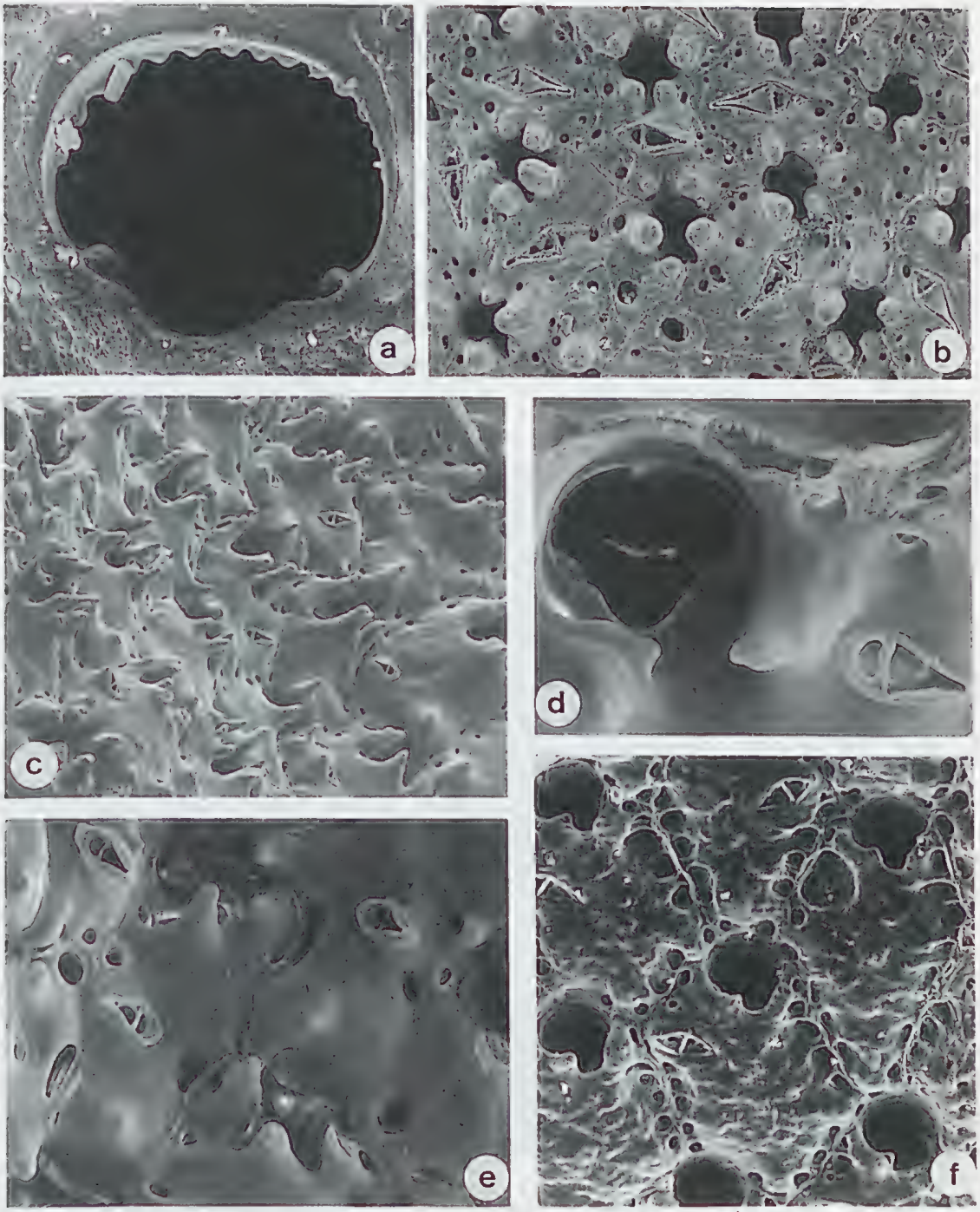


FIG. 31. a,b, *Rhynchozoon haha*; a, ×450; b, ×55. c-e, *Rhynchozoon limatulum*; c, ×70; d, ×300; e, ×140. f, *Rhynchozoon splendens*, ×80.

Rhynchozoon splendens Hayward
(Figs 31f, 32a,b)

Rhynchozoon splendens Hayward, 1988: 335, pl. 13, figs f,g.
Rhynchozoon rostratum: Winston & Heimberg, 1986: 38, figs 95-98.

DESCRIPTION

Colony forming spreading, multilaminar sheets. Autozooids at growing edge oval, convex, separated by distinct grooves; commonly 0.45-0.50×0.3mm. Primary orifice 0.12mm wide, about as long as wide; sinus short, U-shaped, occupying about half proximal width of orifice; condyles indistinct. No oral spines. Frontal wall at first smooth, but becoming coarsely and irregularly nodular; bordered by large and conspicuous marginal pores. Peristomial rim markedly thickened, produced into a series of projecting, knob-like, conical process, the most constant being a medio-proximal pair which may be especially prominent; most autozooids with a single, lateral, suboral avicularium enclosed within the peristome, with triangular, hooked rostrum directed laterally or disto-laterally; the inner proximal corner of the rostral rim is produced as a short, blunt, uncinate process. Small frontal avicularia present, typically one proximo-lateral to peristome, and sometimes a second, more proximally situated; rostrum diamond-shaped, with variable orientation. Ovicell with a short, broad labellum; developing a finely nodular ooecial cover, generally rather inconspicuous.

REMARKS

R. splendens was recently described from Mauritius (Hayward, 1988), where it was found to be common in shallow reef habitats. Comparison of Heron Island specimens with Mauritian material confirms that they are all one species; the shape and size of the primary orifice, the conformation of the peristome, and the characteristic diamond-shaped avicularia are all remarkably similar in the two series of specimens. The species reported from Sanur, Bali, by Winston & Heimberg (1986) as *R. rostratum* (Busk) seems to be *R. splendens*. *R. rostratum* is similar to *R. splendens* in its diamond-shaped frontal avicularia and lobed peristome, which encloses a large lateral-suboral avicularium, but differs in its primary orifice, which has a wide, shallow sinus, and proportionately larger condyles. *R. splendens* was the most common species of *Rhynchozoon* collected at Heron Island; small colonies, and larger sheets, were frequent in eight of the samples described here.

Rhynchozoon tubulosum (Hincks)
(Fig. 32c-e)

Mucronella (?) *tubulosa* Hincks, 1880d: 383, pl. 17, fig. 7.
Mucronella tubulosa: Thornely, 1905: 124.
Rhynchozoon tubulosum: Harmer, 1957: 1064, pl. 65, figs 16-19; Gordon, 1984: 125, pl. 52, figs C-E; Hayward, 1988: 336 [in part; not pl. 14, figs a, b].

DESCRIPTION

Colony forming small, unilaminar patches. Autozooids at growing edge oval to hexagonal, steeply convex, separated by distinct sutures (indistinct in later ontogeny); 0.45-0.5×0.25-0.35mm. Primary orifice as wide as long; proximal edge broadly and shallowly concave between small, rounded, proximo-lateral condyles; distal/disto-lateral denticulations small and widely spaced. Frontal wall irregularly nodular, with few, large, widely-spaced marginal pores; proximal peristomial lip prominent, raised medially as a stout, knobbly mucro, occasionally spiky, or distinctly bifid apically; additional, shorter mucronate processes sometimes developed lateral to the median. Suboral avicularium transversely orientated, on the inner surface of the mucro, the rostrum sharply hooked distally, but without an associated uncinate process. Large frontal avicularia sporadically present, most frequent in older parts of colony; rostrum linguiform, about 0.35mm long, normal to frontal plane and proximally directed. Tiny adventitious avicularia, with short triangular mandible, often developed towards tip of mucro, and rarely elsewhere on the frontal wall. Ovicell about as wide as long, slightly flattened frontally, with a finely tuberculate surface, projecting well above rim of peristome.

REMARKS

With ontogenetic frontal wall thickening the primary orifice becomes deeply immersed and the mucronate proximal peristome especially prominent, so that autozooids appear to be vertically orientated. Hinck's (1880d) unfortunately inadequate figure shows a group of autozooids in late ontogeny, with prominent, mucronate peristomes, tuberculate ovicells clearly visible above the peristome rims, and large, linguiform frontal avicularia. No type specimen is known for *R.*

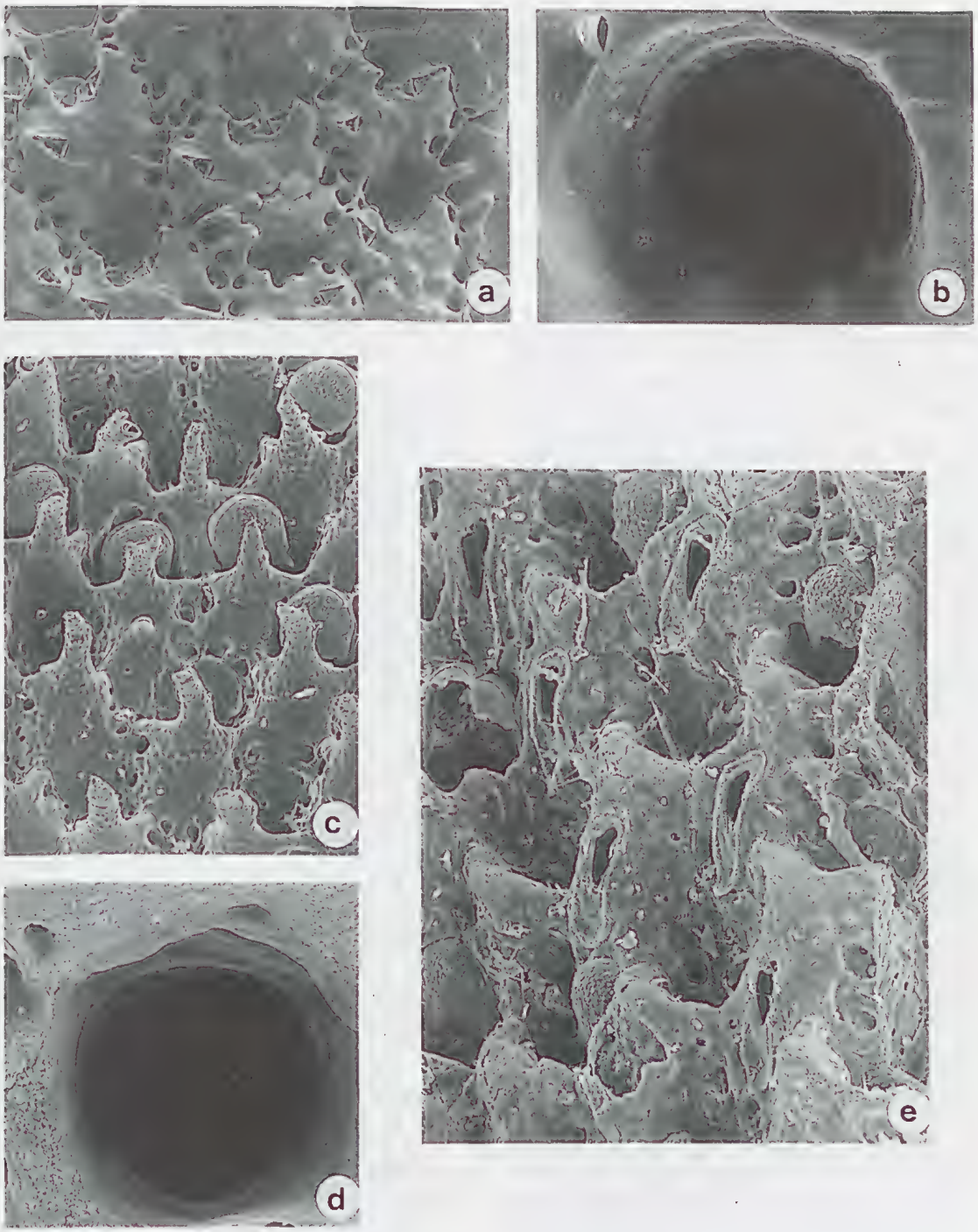


FIG. 32. a,b, *Rhynchozoon splendens*; a, ×60; b, ×350. c-e, *Rhynchozoon tubulosum*; c, ×45; d, ×260; e, ×70.

tubulosum, Hincks' original description is incomplete, and the identity of the Heron Island species described here depends entirely on the resemblance of older autozooids to Hincks' figure. Subsequent authors (see Harmer, 1957: 1064) considered that *Rhynchozoon longirostre* (Hincks), described from southern Australia, was the same as *R. tubulosum*, an assertion which was denied by the author himself (Hincks, 1891). In Hincks' original specimens of *R. longirostre* (e.g., BMNH 1899.5.1.1161, 1163), the suboral avicularium is associated with a massive uncinate process, which partly obscures the primary orifice, a feature not seen in any of the material of *R. tubulosum* examined here. Consequently, the synonymy of the two taxa should be rejected. Thornely's (1905) material of *R. tubulosum* from Sri Lanka (BMNH 1936.12.30.48A) and Harmer's (1957) Indonesian specimens are the same species as that occurring at Heron Island; Harmer's synonymy, however, cannot be accepted until all listed records of *R. tubulosum*, *R. longirostre* and *R. profundum* (MacGillivray) have been re-examined. The material described from Mauritius by Hayward (1988) unfortunately comprised two species, and the specimen figured (Hayward, 1988, pl. 14, figs a,b) is not *R. tubulosum*, but an undescribed species of *Rhynchozoon*.

CONCLUSION

The selection of Bryozoa described in this preliminary account comprises a single cyclostome, and 80 species of cheilostome, encompassing 46 genera in 27 families. Of these 80 species, 14 are new to science and 24 are reported for the first time from Australian seas. The remaining 43 species include at least 25 which are known to be widely distributed in the Indo-West Pacific realm, some of which (e.g., *Chorizopora brongniartii* and *Arthropoma cecilii*) appear to have almost world-wide distributions in shallow tropical and temperate seas. This group of 81 species includes the most abundant, most familiar and taxonomically least problematic members of the bryozoan fauna of the Heron Island reefs. While the range of genera represented gives some indication of the taxonomic diversity of the fauna, the total number of species is likely to be greatly increased as the rest of the collection is studied. It is worth noting that few of the species listed by Livingstone (1927) or described by Hastings (1932) from GBR localities have so far been found in these collections. Unfortunately, progress in taxonomic research on tropical Australian Bryozoa is hampered by the necessity to review all previous published sources critically, and whenever possible to refer to type and original specimens. Harmer's (1957) fourth Siboga Report, presently the most important of these sources, has serious shortcomings in that the synonymies of many of the species it describes can be shown to be erroneous, while a substantial number of others are founded on material which clearly consists of more than a single species.

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FOOT-FLAGGING DISPLAYS OF SOME AUSTRALIAN FROGS. *Memoirs of the Queensland Museum 32(1): 302. 1992:-* Visual displays involving movements of the feet have been recorded for four anuran species: *Hylodes asperus* (Leptodactylidae), *Staurois parvus* (=*tuberilinguis*) and *S. latopalmatus* (Ranidae), and *Taudactylus eungellensis* (Myobatrachidae) (Davison, 1984; Harding, 1982; Heyer et al., 1990; Winter & McDonald, 1986). All of these species are diurnal and live along rainforest streams. This led Heyer et al. (1990) to suggest that visual displays might be a substitute for vocal communication in response to noisy streamside environments where vocal signals are difficult to hear, and may be less risky for frogs that have easy access to a safe refuge. They also noted morphological similarities between *Hylodes asperus* and the Australian hylid *Litoria nannotis*, and questioned whether *L. nannotis* also might exhibit visual displays.

In this note we confirm that *L. nannotis* does exhibit foot-flagging displays, and describe visual displays by three other Australian hylid frogs. These include the first records of nocturnal foot-flagging and foot-flagging displays exhibited outside a rainforest environment. Field observations were made in the wet tropics of northern Queensland and in northern New South Wales, between March 1989 and March 1992.

Litoria genimaculata: Three males were observed displaying on mossy rocks next to Birthday Ck, an upland rainforest stream in Mt Spec National Park. Observations were made over a 15 minute period beginning at 1100h on 16.2.90. One male slowly raised the right rear leg, stretched it out perpendicular to the body and rapidly vibrated the foot on a vertical plane with the toes outstretched. It then leapt onto a second male about 1m away. This second male retreated a further metre and exhibited the same display, once with each rear foot. A third male perched within 50cm then displayed vigorously more than a dozen times, with no apparent sequence of use of the two feet. There followed a series of leaps onto each other, several wrestling bouts, and sporadic displays by all three males until they dispersed approximately 15 minutes after the displays were initiated. All of the males called continuously during these bouts.

Litoria nannotis: Observations were made over a two hour period in November, 1990, on captive specimens maintained in a large aquarium. Visual displays were initiated by a resident male when a second male was placed into the same aquarium. Immediately following the introduction, the resident male called vigorously as he approached the intruder, and then extended the right rear leg out and back in an arc, spreading the toes to reveal the webbing, before returning the leg to the side of the body. This display was repeated continuously with both back legs until the intruder retreated into a crevice. The display was reinitiated each time the intruder appeared. Male *L. nannotis* have been observed in the field to wave their front legs in an arc above the head in similar inter-male displays (A. Dennis, pers. comm.).

Litoria rheocola: Three males were observed displaying along rainforest streams in the vicinity of Mt Finnigan, northern Queensland. All observations were made at night between 2200 and 2330 on 17.12.91. All involved interactions between calling males. The first male was perched on a leaf at a height of 38cm and facing another calling male 40cm away. The first male waved its front right foot twice in an arc over its head. It then made two rapid flicks with the rear leg so that the leg was extended fully, in a lateral plane perpendicular to the long axis of the body, and returned immediately to the side of the body. A second male displayed only with the rear legs, exhibiting seven similar leg flicks in four minutes. Six flicks were with the left leg and one with the right. A third calling male was observed for five minutes and did not display until another male called one metre away. It immediately began displaying with both rear legs in the manner described above. These displays were observed by moonlight.

Litoria fallax: Observations were made between 2150 and 2210h on 01.01.91 in the vicinity of Brays Ck, northern NSW, under well-moonlit conditions. The interaction was between a calling male perched 50cm above the water and a satellite, non-calling male, initially perched 35cm away. The calling male began a rapid clicking encounter call, when approached from behind by the second male. A wrestling bout ensued for approximately one minute during which the first male called continuously and ended with the second male sitting behind and facing the same direction as the first, about 10cm lower on the same branch. The first male then foot-flagged by alternately extending rear legs, starting with a stretch sidewards and slowly moving each leg through a backward arc to end in the lateral resting position. This was repeated seven times, ending when the second male leaped away. The remaining male resumed calling four minutes later. No species reported here has brightly coloured webbing between the toes.

The hylid species reported here to exhibit foot flagging behaviour are all nocturnally active and all use vocalisations to attract conspecific females. Displays were only observed in the presence of rival males. Isolated males, or males in the presence of females, have not been observed displaying.

The functional significance of foot-flagging appears to be related more to male-male aggression than to courtship. Previously reported displays may also prove to have an aggressive rather than a courtship function. More investigations of frog behaviour may reveal a greater diversity of visual displays than previously suspected. Also, observations are required to determine the effect of light intensity (moonlight) on visual displays in nocturnally active frogs.

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A NEW SPECIES OF LIZARD (*TILIQUA*) FROM THE MIOCENE OF RIVERSLEIGH, QUEENSLAND

GLENN M. SHEA AND MARK N. HUTCHINSON

Shea, G.M. & Hutchinson, M.N. 1992 06 29: A new species of lizard (*Tiliqua*) from the Miocene of Riversleigh, Queensland. *Memoirs of the Queensland Museum* **32**(1): 303-310. Brisbane. ISSN 0079-8835.

A new species of *Tiliqua*, *T. pusilla*, is described from fossil dentaries from the Gag locality, Dwornamor local fauna, Middle Miocene of Riversleigh, Queensland. The new species is characterised by its distinctive rounded cheek teeth and very small size. □*Tiliqua, Scincidae, dentition, Miocene, Riversleigh.*

Glenn M. Shea, Department of Veterinary Anatomy, University of Sydney, New South Wales 2006, Australia; Mark N. Hutchinson, South Australian Museum, North Terrace, Adelaide, South Australia 5000, Australia; 24 June, 1991.

The limestone deposits of the Riversleigh area of northwestern Queensland (recently reviewed by Archer et al., 1989) are becoming widely known as a source of excellently preserved vertebrate fossils, ranging in age from the late Oligocene to the Pleistocene. The limestone matrix has enabled acid preparation of delicate bones (e.g. bat skulls) in perfect condition and many thousands of specimens have already been recovered. The detailed preservation and the evident terrestrial nature of some of the faunas are factors suggesting that small reptiles such as lizards, which normally fossilise poorly, would be preserved, and such is the case. Members of the families Agamidae, Varanidae, Gekkonidae and Scincidae have been identified in the collections from Riversleigh. An initial survey of the agamids has just been completed (Covacevich et al., 1990) and we report here on one of the scincid lizards. The Scincidae is the most diverse family in the modern Australian fauna. It includes many highly characteristic forms, suggesting a long period of evolution in Australia about which almost nothing is known. The Riversleigh deposits are the first from the Australian Tertiary known to be rich in fossil skinks (Hutchinson, 1992).

To date, most of the remains identified as lizards are partial or fragmentary lower jaws. These are difficult to identify because there are too few data concerning taxonomic variation in skeletal characters of the very diverse modern Australopapuan fauna. However, one of the most distinctive Australian genera, *Tiliqua* (s.l.), has long been recognised as having unusual teeth (e.g. Smith, 1937), with several of the posterior cheek teeth markedly enlarged and having conical or rounded crowns. Shea (1990) described the *Tiliqua* lineage: a revised *Tiliqua* (including *Trachydosaurus*), plus *Cyclodomorphus*, the latter including the slender species *gerrardii*, *casuarinae* and the *branchialis* complex. Both genera have characteristic dental morphology which allows isolated dental arcades to be identified to species (Archer and Brayshaw, 1978; Bartholomai, 1977; Shea, pers. obs.).

Amongst the material from Riversleigh are two partial dentaries with the enlarged, round-crowned teeth of the *Tiliqua* lineage. These specimens are here described as a new species of *Tiliqua*, the first extinct member of the genus to be described.

MATERIALS AND METHODS

Prepared fossil specimens of lizard jaws were provided by Dr M. Archer, University of N.S.W. These had been sorted from concentrate obtained by the acid processing of limestone blocks from Riversleigh Station, northwest Queensland. Reference material of modern taxa was obtained from the the following collections: American Museum of Natural History, New York; Australian Museum, Sydney; Queensland Museum, Brisbane (QM); Queen Victoria Museum, Launceston; South Australian Museum, Adelaide (SAMA); Western Australian Museum, Perth; Zoologisches Museum, Humboldt Universität, Berlin. Specimens were examined, measured and drawn using a Wild M3Z stereomicroscope with an eyepiece micrometer and drawing tube.

SYSTEMATICS

Family SCINCIDAE

Subfamily LYGOSOMINAE Mittleman, 1952

Tiliqua Gray, 1825

Tiliqua pusilla sp. nov.
(Figs 1-2)

MATERIAL EXAMINED

HOLOTYPE: QM F16876 (formerly M. Archer collection no. AR5337a).

PARATYPE: QM F16877 (formerly M. Archer collection no. AR4183).

TYPE LOCALITY: Gag locality, one of the lowest of the Tertiary System C group of sites on the Gag Plateau, Riversleigh Station, Queensland (precise details of site available from University of NSW Vertebrate Palaeontology Laboratory). Matrix of freshwater limestone. The Gag site has yielded the Dwornamor local fauna and is of probably early Middle Miocene age (c.15 Myr BP; Archer et al., 1989).

DIAGNOSIS

A small species (estimated dentary tooth row length of the holotype, 9mm), cheek teeth enlarged, with crowns blunt and slightly rounded in lingual profile, more conical in mesial profile, apices bearing a shallow central pit from which radiate striae.

DESCRIPTION

HOLOTYPE: (Fig. 1 a-b) A partial left dentary, missing its rostral third and the caudal, non-tooth bearing extremity, including all of the coronoid process and the apex and ventral margin of the angular process. Meckelian groove closed, no trace of suture. Rostral end of ventral margin with a low ridge, presumably the caudoventral extremity of the symphysial crest. Apex of splenial notch (rostral margin of inferior alveolar foramen) lies at midpoint of interval between coronoid border of dorsal medial lamina and caudal margin of symphysial crest. Coronoid margin of dorsal medial lamina obtusely angulate. Lateral surface with a deep, well-defined arcuate muscle scar caudal to level of last tooth, presumably for the M. adductor mandibulae externus superficialis (AMES) (part IV, Wineski and Gans, 1984).

Internal septum fused ventrally along entire length to ventral medial lamina, completely separating inferior alveolar canal from Meckelian canal. Caudal margin of internal septum with two notches (caudodorsal and rostroventral) for articulation with surangular.

Labial wall of dental sulcus tall and robust, lingual wall almost absent, but lingual margin well-defined and sharply angulate. Dentition pleurodont. Seven closely-packed teeth of even occlusal height and two unfilled tooth loci present, in order from mesial to distal: a tooth locus for a similar-sized tooth to those immediately caudal, at the level of the caudal extent to the ventral symphysial crest; a tooth, missing crown, with a small resorption pit at base; an intact, unresorbed tooth; a tooth largely resorbed at the base, but with intact crown; a tooth with a small resorption pit basally, but with mesial margin of crown missing; a very large empty tooth locus for a tooth approximately twice the diameter of the preceding teeth; a large tooth (only slightly less in diameter than the preceding locus) with intact crown, but with a large resorption pit basally; two intact teeth, the second with a small resorption pit, both abruptly narrower and shorter (occlusal surface lower) than the preceding tooth. Tooth crowns bluntly rounded in lingual profile, slightly more conical in mesial profile, the largest extant tooth even more flattened; mesial teeth with a shallow apical notch, from which striae radiate towards the periphery of the crown; similar, shallower striae present on more caudal teeth.

PARATYPE: (Fig. 1 c-d) The entire rostral half of a left dentary, broken at the level of the 11th tooth and apex of splenial notch, but with most teeth either broken or missing. The portion overlapping with the holotype (tooth loci 5-11) is similar to it in all respects, but slightly smaller. In dorsal view, dentary nearly straight. Symphysis flattened, angle between symphysial surface and lingual surface obtuse, slightly rounded. Angle between mandibles (as estimated by apposition of a mirror image) 41° internally, 50° externally.

Lateral surface with six irregularly spaced mental foramina. Teeth and loci are present as follows, from mesial to distal: Five teeth, obliquely fractured at base to leave only the implanted portion, the fifth level with the end of the ventral symphysial crest; a tooth missing lateral surface of crown; an empty tooth locus of similar size to the preceding teeth; a tooth broken transversely at level of margin of mandible, missing entire crown; an entire, unworn tooth with a fracture line below the crown; a very large empty tooth locus for a tooth approximately twice the diameter of the preceding teeth, and a large tooth stump, similar in diameter to the preceding empty tooth locus, missing crown. Resorption pits are present in the bases of the second, fifth, eighth and eleventh teeth. The single intact tooth (ninth) slanting labially about 30° from vertical. In mesial profile, lingual wall nearly straight, labial wall of crown slightly bulbous, apex moderately narrow, conical, but with a prominent mesiodistal apical notch. In lingual view, crown more rounded, slightly

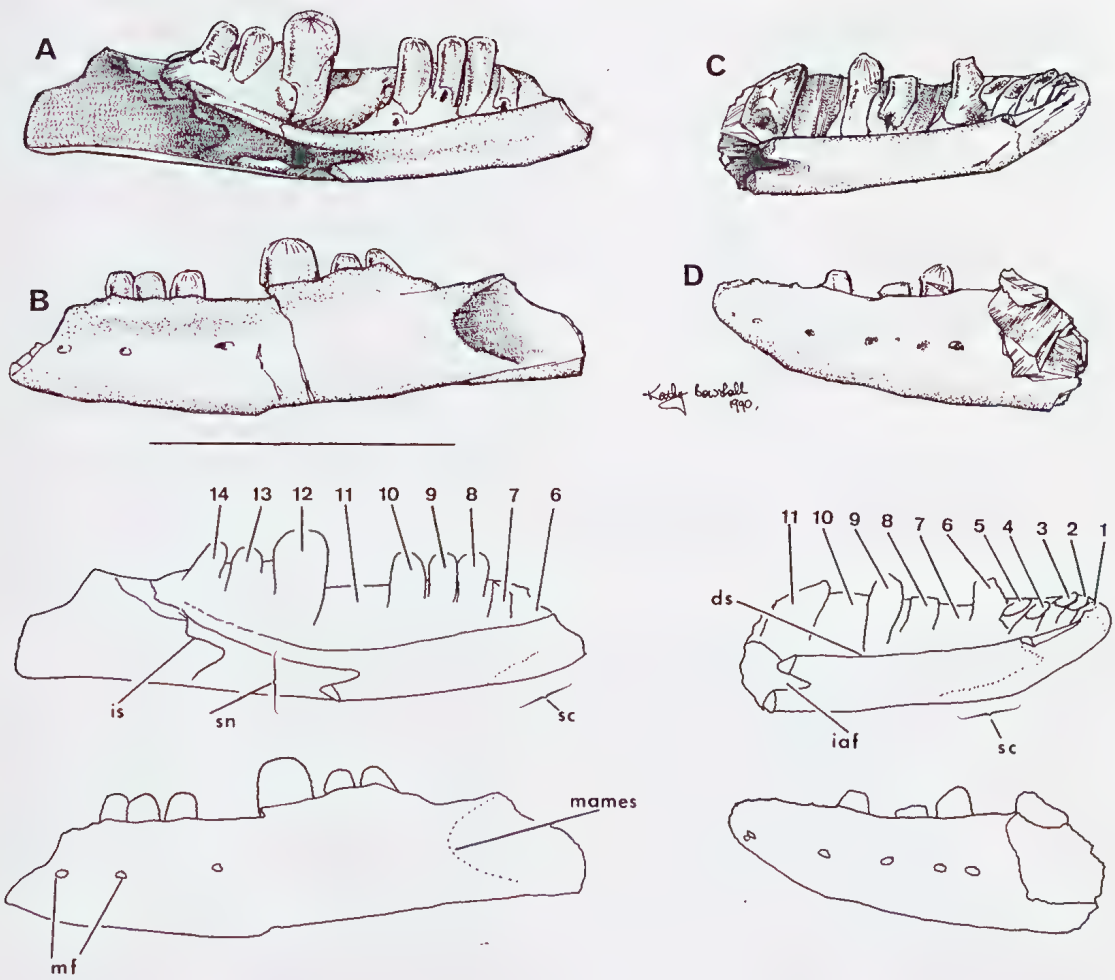

FIG. 1. *Tiliqua pusilla* sp. nov. Holotype (QM F16876, A-B) and paratype (QM F16877, C-D) partial left dentaries in lingual (A, C) and labial (B, D) views. Scale bar equals 5mm. Abbreviations: ds, dental sulcus; iaf, inferior alveolar foramen; is, internal septum; mames, scar for mandibular adductor musclulature; mf, mental foramina; sc, symphysial crest; sn, splenial notch; numbers indicate tooth positions.

higher distally. Crown with radiating striae in occlusal view.

Etymology

From *pusilla*, Latin adjective meaning very small.

Comparison with other Taxa

The closed Meckelian groove of *T. pusilla* is a synapomorphy of both the *Egernia* and *Eugongylus* groups within the subfamily Lygosominae (Greer, 1979). Within these two groups, presence of enlarged teeth in the caudal part of the dental arcade, with the tenth or subsequent dentary tooth largest, is a synapomorphy of the *Tiliqua* lineage (Shea, 1990).

Both specimens are nearly identical in size and morphology and presumably come from different individuals of the same species. The difference in shape of the tooth crowns in mesial profile is probably due to wear in the holotype. The paratype is complete enough to determine that the tenth and (especially) the eleventh teeth are enlarged and, by matching the positions of the symphysial crest and inferior alveolar foramen, it is possible to overlay the two specimens to show that the large tooth preserved in the holotype is the twelfth. Figure 2 shows a composite restoration of the mandible.

Tiliqua pusilla differs from all but one of the

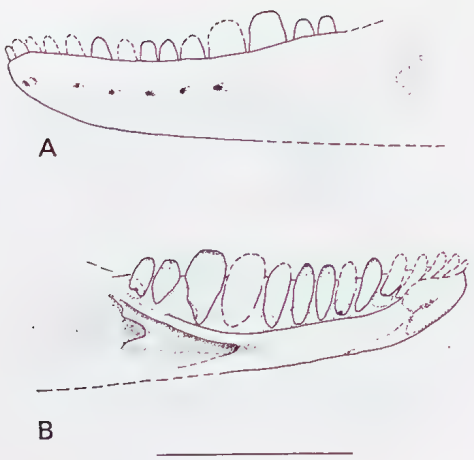

FIG. 2. *Tiliqua pusilla* sp. nov. Diagrammatic restoration of left dentary (A, labial view. B, lingual view) based on holotype and paratype specimens. Scale bar 5mm.

modern species of *Tiliqua* in its lesser size and also in tooth shape. With an estimated dentary tooth row length of 9mm, the holotype is smaller than even neonates of all *Tiliqua* except *T. adelaidensis* (neonate dentary tooth row length of other *Tiliqua* >10mm; neonate dentary tooth row length of *T. adelaidensis* not known, but adult dentary tooth row length of *T. adelaidensis* (8.2-9.3mm, n = 3). Based on the proportions of living members of the *Tiliqua* lineage, this tooth row length indicates a midline skull length of no more than 20mm. Of the seven other species of *Tiliqua*, *T. nigrolutea*, *T. occipitalis* and *T. rugosa* (Fig. 3 a-c) have conical tooth crowns in both lingual and mesial profiles, with a cutting edge directed obliquely across the crown. *T. multifasciata* (Fig. 3d), while having lower, broader teeth, also has a conical apex to the crown, but with a pronounced apical notch. *Tiliqua adelaidensis* (Fig. 3e), while more similar in size to *T. pusilla* has teeth with parallel sides, capped by a low, angulate crown in lingual profile, and slightly compressed in mesiodistal view. *Tiliqua scincoides* and *T. gigas* (Fig. 3f-g) have rounded crowns to the largest teeth and slightly more conical crowns to the more mesial teeth, but in both species a low crest obliquely crosses the occlusal surface. In *T. pusilla*, a distinct notch is present, both on the single unworn tooth of the paratype, and the slightly more worn teeth of the holotype.

Tiliqua pusilla also differs in dental morphology from *Cyclodomorphus*. The teeth of the *C. branchialis* complex (Fig. 3h-i) and *C. casuarinae* (Fig. 3j) have more acutely conical crowns, with the apex towards the distal margin in lingual profile, or even slightly distally recurved. The other two *Cyclodomorphus* species, *C. gerrardii* (Fig. 3k) and *C. maximus*, have very rounded crowns to the largest teeth. In *C. gerrardii*, the teeth are more widely spaced, and the single enlarged tooth is both grossly larger than adjacent teeth, and much lower than in *T. pusilla*. In *C. maximus*, the teeth lack the apical notch and are relatively narrower relative to their height. Further, the mandible of *C. maximus* is relatively more gracile, which is reflected by the much narrower splenial notch in the caudal part of the dentary, and the dentary is larger overall.

Our placement of the species in *Tiliqua* rather than *Cyclodomorphus* is based on one synapomorphy and one character of uncertain polarity. *Tiliqua pusilla*, like modern *Tiliqua*, has a long, low, ventral symphysial crest, extending caudally to the level of the fifth tooth. *Cyclodomorphus* and the closest outgroup to the *Tiliqua* lineage, *Egernia* (Shea, 1990), have a much shorter crest, which may project medially giving a hooked outline. Secondly, the angulate nature of the coronoid margin of the dorsal medial lamina is similar to that seen in modern *Tiliqua*, where it is due to enhancement of a medial buttress on the rostral process of the coronoid. In most *Cyclodomorphus* and *Egernia* the buttress is less developed and more oblique, leaving a more evenly sloping coronoid margin to the dentary.

Tiliqua pusilla is unusual compared with living *Tiliqua* in two features: its small size and the low number of dentary teeth. Both small adult size and reduced number of dentary teeth are common in *Cyclodomorphus*. Thus an explanation for the similarity between *T. pusilla* and *Cyclodomorphus* is needed. The first possibility is that the similarity in size and reduced tooth number is because the specimens of *T. pusilla* are juveniles. However, the specimens are clearly not juvenile as they have a well-defined dental sulcus with a sharply angulate lingual margin, two large teeth and the more mesial teeth subequal in size and showing several cycles of tooth replacement. In juveniles of all *Tiliqua* and *Cyclodomorphus* species, the dental sulcus is poorly-defined, its lingual margin blending with the adjacent dorsal medial lamina. There is only a single large tooth, and the teeth mesial to this one show a distinct alternation in size (Shea, MS).

Since both specimens are adult, the number of dentary teeth is lower than for adults of other *Tiliqua* species, which have more than 14 dentary

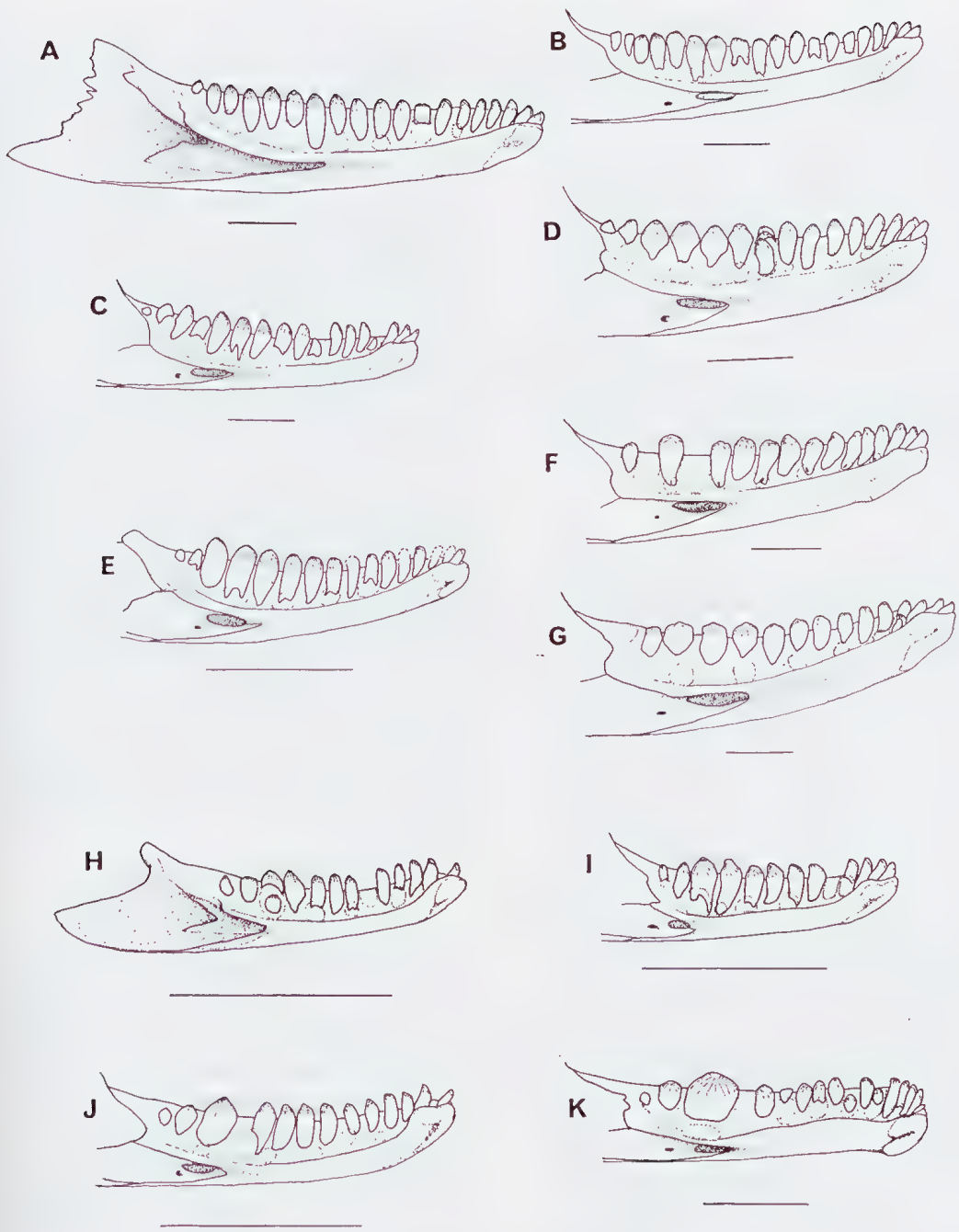

FIG. 3. Lingual views of dentaries of living species of the *Tiliqua* lineage showing variation in proportions, tooth number and shape. A and H are isolated dentaries showing the internal structure and E lacks the coronoid; the remainder are intact mandibles. A, *T. rugosa* (SAMA R27584). B, *T. occipitalis* (SAMA R35758). C, *T. nigrolutea* (SAMA R2725). D, *T. multifasciata* (SAMA R35757). E, *T. adelaidensis* (SAMA R8589). F, *T. scincoides* (SAMA R27037). G, *T. gigas* (SAMA R11419). H, *Cyclodomorphus* cf *branchialis* (SAMA R38021). I, *C. melanops* (SAMA R37565). J, *C. casuarinae* (SAMA R35682). K, *C. gerrardii* (SAMA R35761). Scale bars 5mm.

teeth, and show a progressive distal shift in the number of the largest tooth with age, as estimated by increasing size (Shea, MS). In the *Tiliqua* lineage the two attributes (small size, reduced tooth count) are probably linked since in order to have teeth of sufficient absolute size, small species of the *Tiliqua* lineage may have to make do with fewer teeth overall in each dental arcade. Compared with the similarly-sized *T. adelaidensis*, *T. pusilla* has larger but fewer teeth (14, 11-12 largest, versus 16, 12-14 largest) and a more heavily-built jaw, and was evidently more strictly adapted for durophagy than *T. adelaidensis*, which has thinner, sharper-crowned teeth. This comparison supports the idea that the low number of teeth in *T. pusilla* is a consequence of allometric scaling, with a limit to reduction in tooth size of crushing teeth imposed by the necessity of preserving tooth strength.

Discussion

Tiliqua is one of the most characteristically Australian scincid genera. Morphologically (Greer, 1970, 1979; Shea, 1990), biochemically (Hutchinson, 1981; Baverstock and Donnellan, 1990) and karyologically (Donnellan, 1985), the only living relatives of *Tiliqua* are *Cyclodomorphus*, *Egernia* and *Corucia*, collectively comprising the *Egernia* group (Greer, 1979). Little is known of the history of *Tiliqua* (or of any other skink genus) in Australia.

Tiliqua has been recorded numerous times from Pleistocene to Recent deposits (Krefft, 1867, 1870, 1871; Stirling, 1889; Hale and Tindale, 1930; Tindale, 1933; Cook, 1960, 1963; Mulvaney, 1960; Mulvaney et al., 1964; Trezise, 1970; Lampert, 1971; Thorne, 1971; Marshall, 1973; Bowdler, 1974; Ryder, 1974; M. J. Smith, 1976, 1982; Bartholomai, 1977; Hope et al., 1977; Archer and Brayshaw, 1978; Molnar, 1978, 1982; Williams, 1980; Hope, 1981; M. A. Smith, 1982; Wells et al., 1984) but is almost unknown from the Tertiary. There is one record from the Pliocene Wellington Caves (Hand et al., 1988) and one from the Miocene, based on a statement by Estes (1984) that a specimen of *Tiliqua* had been identified by J. Gauthier among the Kutjamarpu local fauna (Middle Miocene of northern South Australia; Stirton et al., 1967). Both records remain undescribed. The Kutjamarpu local fauna is considered (Archer et al., 1989) to be just older than the Dwornamor local fauna, making the former the the oldest record of the *Tiliqua* lineage. The existence of this specimen in South Australia and *T. pusilla* in Queensland shows that the *Tiliqua* lineage was widespread in Australia by the Middle Miocene.

Identification of the Riversleigh species as *Tiliqua* rather than *Cyclodomorphus* suggests that these sister taxa had diverged prior to the Middle Miocene, pushing the diversification and ultimate origin of the *Egernia* group even further back, potentially to pre-Miocene times. This scenario is incompatible with a previous hypothesis for *Egernia* of rapid Pleistocene speciation following a Pliocene origin (Horton, 1972). A preliminary dating via the 'albumin clock' of around 12 Myr BP for the *Egernia- Tiliqua* split (Baverstock and Donnellan, 1990) is thus also too recent.

The mammal fauna of the Dwornamor local fauna is dominated by arboreal browsers and has a very high diversity (Hand, 1985: Archer & Flannery, 1985; Flannery & Archer, 1987a; 1987b; Archer et al., 1988) with minimally 58 species present (Archer et al., 1989, Table 1). Such diversity would today be found only in a rainforest environment, which has supported the idea of the Dwornamor local fauna as a tropical rainforest fauna. With the exception of *T. gigas*, living species of *Tiliqua* do not inhabit rainforests, so that *T. pusilla*, combining small size and rainforest-dwelling habits, represents a radiation of the genus with no modern parallel. Possibly *Tiliqua* was a more diverse taxon in the past, and/or modern bluetongues represent a recent open-country radiation descended from dwarfish rainforest ancestors.

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PERMIAN ECHINODERMS FROM WESTERN AUSTRALIA

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A new study of the Permian echinoderms of Western Australia included field collection and restudy of several earlier collections. Significant morphologic and stratigraphic details are provided about previously described taxa. New taxa are the crinoids: *Neocamptocrinus barrabiddyensis, N. millyitensis, Stomiocrinus merlinleighensis, Neoplatycrinus callytharaensis, N. miamiaensis, Wrightocrinus wooramelensis, Litocrinus pansus, L. protuberans, Lampodosocrinus variabilis, Cosmetocrinus? middalyaensis, Spheniscocrinus australis, Minilyacrinus williamburyensis, Texacrinus goochensis, T. hardmanensis, T. gascoynensis, Galateacrinus australis, Cymbiocrinus cherrabunensis, Jimbacrinus donnellyensis,* and *Baryschyr? carnarvonensis* and the blastoids *Neoschisma extensum,* and *Rhopaloblastus cuspidus* and the stellaroid *Monaster coleyi.* Echinoid remains are recorded for the first time in the Permian of Western Australia. Ranges of several Carboniferous crinoids are extended into the Permian, including a coelocrinid and pentameric stem-bearing forms. The youngest Palaeozoic crinoids known are described from the Tatarian Hardman Formation of the Canning Basin.

Echinoderms in the Callythara Formation include 16 camerates, 37 inadunates, and 1 flexible among the crinoids, 5 blastoids, and 1 echinoid. Younger Permian strata yielded 3 camerates, 12 inadunates, 1 blastoid, and 1 starfish. Lineages of *Neocamptocrinus, Neoplatycrinus, Texacrinus, Jimbacrinus, Tapinocrinus,* and *Stomiocrinus* are recognised and offer potential for additional correlation of Permian strata throughout Western Australia. □ *palaeontology, Crinoids, Permian, Western Australia.*

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Echinoderms from the Permian of Western Australia were first recorded from crinoid stems by Foord (1890) who described them from the Gascoyne River bed and by Etheridge (1903) who reported an endophytic fungal infestation of some crinoid columnals from the northern Carnarvon Basin. Teichert (1949, 1954) and Webster (1987, 1990) on crinoids, Breimer & Macurda (1972) on blastoids and Kesling (1969) on starfish provide the only detailed works on the fauna to date; Teichert (1951) gave a useful summary of the fauna as he knew it then. This paper describes new crinoids and blastoids as well as providing much new information on known species and recording echinoid remains for the first time. Fossil echinoderms are known from the Permian of the Perth, Carnarvon (previously referred to as the Northwest Basin and Canning Basins with the oldest occurring in the Sakmarian to Artinskian of the Carnarvon Basin and the youngest in the Tatarian of the Canning Basin. Echinoderm fossils dealt with herein include a crinoid cup from the Fossil Cliffs Formation of the Perth Basin, and a few crinoid and blastoid specimens from the Noonkanbah and Hardman Formations of the Canning Basin but principally derive from the Carnarvon Basin where the Callytharra Formation has yielded the most prolific echinoderm fauna.

Permian geology and stratigraphy of Western Australia has been detailed through the regional mapping efforts, since the late 1940s, of the Bureau of Mineral Resources and the Geological Survey of Western Australia in the 1:250,000 geological map series of the BMR. These results owe some of their success to earlier reconnaissance work of several people but in the context of Permian palaeontology that of Teichert was most significant. He contributed numerous papers and reports but none more significant than his landmark study (Teichert, 1949) on the crinoid *Calceolispongia* and biostratigraphic utility of its distinctive species. This work provided an intrabasinal biostratigraphic scheme for the Carnarvon Basin which remains virtually unchanged today. Studies of the Ammonoidea (several papers listed in Quilty, 1975) have been used to provide an international correlation. Summaries of the geology and stratigraphy were provided by the

Geological Survey of Western Australia (Playford et al., 1975), for the Carnarvon Basin by Condon (1954, 1967), and for the Canning Basin by Veevers & Wells (1961). We have confined our study to palaeontology and relied heavily upon these earlier works as a framework within which to place our findings. A generalised locality map and stratigraphic columns of the Carnarvon and Canning Basins were given in Webster (1990).

PRESERVATION

At Callytharra Springs most echinoderm material is disarticulated except for microcrinoids, microblastoids, and pleuricolumnal sections of stems. A few exceptions of articulated cups of crinoids and blastoids are known but disarticulated plates of these species are also found associated. Associated but disarticulated cup plates, brachials and columnals of particular species are present on the outcrop indicating minor displacement but definite disaggregation by currents or bioturbation. Distortion and fracturing, resulting from compaction, is most common in large relatively thin ossicles or thinner parts of more robust faunal elements. This is most noticeable on large camerates such as *Neoplatycrinus* and the stem of *Neocamp-tocrinus*, a result of the ease of seeing such features on the larger faunal elements. Careful collecting and microscopic investigation show that this also occurs in smaller elements of the fauna.

To the north, exposures of the Callytharra Formation from the vicinity of Mt Sandiman through Williambury Station and into the Gooch Range show carbonate grainstones with minor marls and shales forming hogback ridges with the formation tilted, usually to the west and eroded. Large pluricolumnals, dominated by *Baryschyr*? *carnarvonensis* sp. nov. up to 10cm long, are common in the lower part of the Callytharra Formation. Articulated crinoid cups and crowns, although rather infrequently found, occur on bedding surfaces. Specimens are exceedingly difficult to extract because they are the same hardness as the enclosing grainstones. Most specimens tend to weather at the same rate as the matrix and solution weathering of ossicles often precludes identification. The articulated crowns, often with proximal stem attached, deny postmortem transportation. Most are considered to have died in situ; the cause of death is not apparent. The matrix shows no graded bedding that could imply debris flows or tempestites, but bioturbation is obvious in some grainstones.

Considerable time walking bedding planes and looking at weathered scree, is required to find the rare good specimen. Rarely, sets of arms and crowns are found weathering from thin interbeds of shale or marl. We suggest that numerous crinoid species are to be found in these northern exposures of the Callytharra Formation with careful and patient collecting.

FAUNAL ANALYSIS

The faunal list of our collection from the Callytharra Formation (Table 1) shows that we found most of the species recorded by Webster (1987) except for *Tapinocrinus macurdai*, *T. ingrami*, *T.* sp., *Actinocrinites* sp. cf. *A. brouweri* and a few of the unidentified camerate and inadunate radials.

The Callytharra fauna contains 16 camerate species, 37 inadunates and 1 flexible. As briefly summarised by Webster (1987), most Permian crinoid faunas worldwide are dominated by inadunates. Only the Timor and possibly Bolivian faunas contain significant camerates and flexibles. The Callytharra fauna is the second most diverse Permian fauna in the world after Timor but the virtual lack of flexibles leads us to suggest that the flexibles could not adapt to the cooler water environment of the Australian Permian.

In this paper 2 camerates and 12 inadunates are added to the faunal list as outlined by Webster (1987). These include three holdover genera, a coelocrinid (*Dorycrinus*), barycrinid indet., and *Cosmetocrinus*, not previously recorded from the Permian (Moore & Teichert, 1978). The youngest possible ancestors are to be found in the Early Carboniferous of North America. The new inadunates include *Minilyacrinus* gen. nov. and new species of *Lampadosocrinus, Texacrinus, Galateacrinus* and *Baryschyr*? not previously recorded in the region. Only *Texacrinus* was previously reported from the Permian. The microcrinoids described are the first described from Australia. *Wrightocrinus, Litocrinus* and Timorechinidae indet. are known from Timor thus strengthening faunal links between the two areas.

The Basleo fauna of Timor is the most diverse Permian crinoid fauna known in the world. It contains 232 species as opposed to the 56 species so far recorded in the Callytharra Formation. Although study of the Timorese collections housed in European museums leads one of us (GDW) to believe that restudy of the inadunates may reduce the number of species recognised it will remain an incredibly diverse fauna. Teichert (1951) con-

	QML757	QML758	QML759	QML760	QML761	757-761
indet. platycrinitid or dichocrinid radial	1		1		1	
Actinocrinites cf. *A. brouweri*						
Platycrinites wrighti				1		
Neoplatycrinus callytharaensis		6	8		1	15
Pleurocrinus? sp. -radials (basals)	25(16)	2		4		
Neocamptocrinus sp.	8	17	32	10	4	14
indet. dichocrinid radials 1-3	17	5	5	6	1	5
indet. camerate radials 1-5	10		6	2		4
Notocatillocrinus callytharaensis (partials)	2(36)	2(1)	(10)	(2)		1(11)
Synbathocrinus campanulatus (partials)	9	3(1)	2(2)			1(2)
Synbathocrinus constrictus (partials)	2(6)	1				(1)
Cydonocrinus cf. *C. tuberculatus* partial	1					
Tapinocrinus macurdai						
Tapinocrinus ingrami						
Tapinocrinus sp.						
Parabursacrinus magnificus (radials)	(150)	(67)	(77)	(23)	1	(86)
Parabursacrinus granulatus radials	15					
Parabursacrinus nefotassiensis radials	16	7	4	1		1
Calceolispongia spinosa basals	10	5(brachs)	11	1		3
Calceolispongia cf. *C. spinosa*						
Calceolispongia digitata basals	10	7	4	6	2	7
Calceolispongiidae sp. indet.						
indet inadunate radials 1-10	45	9	24	5	3	13
indet. flexible radial			1			
Apographiocrinus pumilus brachials	1			2		2
Phosphannulus pluricolumnals	15					
Radials (unidentified)	169	33	35	14		34
Tegmen spines	21	2	15		4	4
Radials with ribs	7			9		
Neocamptocrinus radials	1					
Infrabasal or basal circlet	30	9	12	4		6
Columnals (unidentified)	many	many	many	many	many	many
Barycrinidae? indet. pentameric pluricolumnals	15			3		
Neoschisma verrucosum plates	4			1		
Neoschisma extensum plates	41	3	6	8		7
Notoblastus stellaris plates	18		17			

TABLE 1. Fauna of type section of Callythara Formation west of Callythara Springs on Wooramel River giving specimen numbers from field collections by the authors. Numbers in parentheses refer to partial cups or specific cup plates where both complete and partial cups were found.

sidered the Western Australian fauna closely allied to that of Timor but, with the exception of *Calceolispongia* he regarded the Western Australian fauna as an impoverished Timor fauna without indicating any reason for the impoverishment. We suggest that the Timor fauna lived in a

	Callytharra	Coyrie	Bulgadoo	Cundlego	Quinnanie Sh.	Wandagee	Fossil Cliffs	Noonkanbah	Cherrabun Mbr
Neocamptocrinus millyitensis									x
Neocamptocrinus occidentalis				x					
Neocampto. barrabiddyensis			x						
Stomiocrinus ferruginus						x			
Stomiocrinus merlinleighensis			x						
Texacrinus hardmanensis									x
Texacrinus gascoynensis				x					
Texacrinus goochensis	x								
Skaiocrinus granulosus						x			
Jimbacrinus minilyaensis						x			
Jimbacrinus bostocki				x					
Jimbacrinus donnellyensis			x						
Cymbiocrinus cherrabunensis									x
Trautscholdicrinus sp.							x		
Occiducrinus australis						x			
Rhenocrinidae gen. nov.						x			
Eoindocrinus praecontignatus						x			
Tapinocrinus spinosus						x			
Family and genus indet.						x			
Anechocrinus nalbiaensis					x				

TABLE 2. Lineage chart and stratigraphic distribution of the echinoderm fauna of the post-Callytharra Fmn Permian of WA. Taxa from Teichert (1949) are not included as they were well placed stratigraphically in the original work. Callytharra through Wandagee Fmns are in stratigraphic sequence for the Carnarvon Basin. The Fossil Cliffs Formation of the Perth Basin is temporally equivalent to the Callytharra Fmn. The Noonkanbah Fmn (equivalent to the Coyrie through Wandagee Fmns) and Tatarian Cherrabun Mbr, Hardman Fmn are in the Canning Basin.

warm water environment favourable to a higher carbonate productivity. In contrast the abundant clastic sedimentation of the Western Australian Permian and the type of sediment suggest not only nearer shore, more turbid environments but also cooler water environments with less carbonate production. The cooler water environment of the Permian deposits of Western Australia were recognized by Condon (1967) and Dickins (1978) among others. We consider the echinoderms of the Western Australian Permian to be those that could adapt better to the greater diversity of environments and note that a few are unknown in Timor (*Texacrinus*, *Cosmetocrinus* and the coelocrinid).

The post Callytharra crinoids of Western Australia, following the work of Teichert (1949, 1954), Webster (1990) and this paper, number 3 camerate and 12 inadunate genera. These forms occur mainly in sandstone or shale with rare exceptions such as *Stomiocrinus merlinleighensis* and *Jimbacrinus donnellyensis*. Many occur in clusters with multiple specimens of few species along bedding planes. Many specimens were disaggregated in part indicating postmortem current or scavenger activity. Cross-bedding, scour and fill and ripple marks were observed in these sandstones recording current activity. Bioturbation is evident but not extensively.

Crinoids of the Cherrabun Member, Hardman Formation in the Canning Basin (Table 2) are among the youngest Palaeozoic crinoids known. The age of this horizon, which also yielded the ammonoid *Cyclolobus persulcatus* Rothpletz, 1892, is discussed by Glenister et al. (1990) as Dzhulfian (i.e. within the Tatarian of the European scale). All three species represent lineages common in the Carboniferous of North America. *Cymbiocrinus* is known from the Permian of Thailand (Webster & Jell, in prep.); *Neocamptocrinus* is known only from Australia (Willink, 1980; Webster, 1990; herein).

LINEAGES

Teichert (1951) considered that only one crinoid showed a lineage of stratigraphic utility in Western Australia. Based on knowledge at the time his view was correct. However, the added information from the Callytharra and younger fauna reveals several parallel lineages; some may have biostratigraphic utility through Western Australia, the rest of Australia and even to Timor and India. The *Calceolispongia* lineage detailed by Teichert (1949) remains the most useful for Western Australia but it also needs revision in the light of extensive new collections and its potential for correlation in the Canning Basin has yet to be addressed.

Other lineages that we recognise in Western

Australia (Table 2) are species within each of *Neocamptocrinus, Neoplatycrinus, Texacrinus, Jimbacrinus, Tapinocrinus* and *Stomiocrinus*. Although these are considered independently it should be noted that *Neocamptocrinus, Neoplatycrinus* and *Calceolispongia* occur together at most horizons in the Permian of Western Australia suggesting that they needed similar living conditions.

Stems of *Neocamptocrinus* are found in most horizons with marine fossils from the Callytharra to the Hardman Formations. They have not been studied in detail. Specimens that we have observed show greatest size in the Wandagee Formation (Artinskian) (Fig. 3M,N). Cups, thecae and crowns of *Neocamptocrinus* are uncommon. They are known from the Bulgadoo Shale *N. barrabiddyensis* sp. nov., from the Cundlego Formation, *N. occidentalis*, and from the Hardman Formation, *N. millyitensis*. These three species are considered an evolutionary lineage with *N. occidentalis* evolving from *N. barrabiddyensis* by elongation of the cup with nearly vertical walls distally. In turn, *N. millyitensis* evolved from *N. occidentalis* with a more flattened basal circlet, reduction in the number of plates in the anal series above the primanal and modification of the ornament on tegmen plates. Webster (1990) discussed the relationship of *N. occidentalis* and *N.* n. sp. (=*N. millyitensis*) with eastern Australian species (Willink,1980).

Stomiocrinus merlinleighensis in the Bulgadoo Formation could be the ancestor of *S. ferruginus* in the Wandagee Formation by enlargement, modification of the arms by shortening and thickening the brachials and reduction of the relative size of the orals. Timor species of *Stomiocrinus* are probably derived from *S. merlinleighensis* by modification of oral plates and flattening of the tegmen. *Stomiocrinus* is unknown in eastern Australia.

Evolution of *Neoplatycrinus miamiaensis* from *N. callytharraensis* by modification of the ornament from one large prominent node to several large nodes and probably flattening of the basal circlet forming a low bowl-shaped cup. The "twist" nodals and internodals currently assigned to *Platycrinites/Neoplatycrinus* spp. and commonly found associated with the disarticulated plates of *Neoplatycrinus* probably belong to the genus. Unfortunately they were probably static in evolution during the Early Permian and show no significant differences or evolutionary trends. Although not reported, "twist" columnals are present in the Oxtrack Formation of the Cracow area, Queensland. Additional study of the platycrinid columnals of Australia is needed to fully evaluate their stratigraphic potential.

The tapinocrinids are known from Western Australia and Timor. In Western Australia, *Tapinocrinus macurdai* and *T. ingrami* are known from the Callytherra Formation with the former the likely ancestor of *T. spinosus* from the Wandagee Formation and Basleo fauna of Timor. Development of *T. spinosus* was by flattening of the cup into a disc shape, enlargement of the radials into a blunt spine and loss of granular ornament. Although the spine did not develop, *T. timoricus* also lost the ornament and developed a discoid cup. There is no record of *Tapinocrinus* in eastern Australia.

The texacrinids are represented in Western Australia by four species starting with *T. goochensis* in the Callytharra Formation followed by the more robust *T. gascoynensis* in the Cundlego or Wandagee Formation. No further form of this heavier stock is known. *Skaiocrinus granulosus* is a more elongate form with or without slightly peneplenary radial facets and pinnules with longitudinal ridges. The youngest form *T. hardmanensis* is a slender elongate form which may have evolved through *T. goochensis* from the same stock as *S. granulosus*. Texacrinids are unknown in eastern Australia.

Teichert (1949) considered the origin of *Calceolispongia* to be uncertain but perhaps derived from the Cromyocrinidae. Moore *et al.* (in Moore & Teichert, 1978) suggested that the Calceolispongidae were derived through the Cymbiocrinidae or Ampelocrinidae. We consider the Cymbiocrinidae line to be most likely based on the bowl-shaped cup, large single anal and cuneate arms. The lineage of *Jimbacrinus* is not as clear as that of *Calceolispongia* but may include a sequence from Calceolispongidae? sp. (Webster, 1987) from the Callytharra Formation to *J. donnellyensis* in the Bulgadoo Shale to *J. bostocki* Teichert, 1954 in the Cundlego Formation to *J. minilyaensis* Webster, 1990 in the Wandagee Formation and possibly to *Cymbiocrinus cherrabunensis* in the Hardman Formation.

Webster (1987) noted the resemblance of Calceolispongidae? sp. to the calceolispongids but considered differences in the lack of bulbous basals and presence of an isotomous branching on the third brachial in one ray. If the branching had been on the second brachial the specimen would have been assigned to *Cymbiocrinus*. Calceolispongidae? sp. probably derived from the same ancestor as *Calceolispongia*. *J. donnellyen-*

sis may have evolved from Calceolispongidae? sp. by thickening of the basals and loss of arm branching. In turn *J. bostocki* evolved by development of the spines on the bulbous basals whereas *J. minilyaensis* has a reduction in the bulbous basals, possibly representing a different lineage from Calceolispongidae? sp. *Cymbiocrinus cherrabunensis* is related to the calceolispongids mostly by the bulbous basals; the arm branching pattern, however, is not typical of that family.

The second largest Permian crinoid fauna of the Carnarvon Basin occurs in the Wandagee Formation in the east limb of a syncline on the north bank of the Minilya River, approximately 10km westnorthwest of Wandagee Homestead. This locality is the type locality for several species of *Calceolispongia* (Teichert,1949) and other crinoids (Webster,1990). Some confusion about the stratigraphy has resulted from nomenclatural changes. Teichert (1949) considered the Wandagee Formation to include the unit later named the Quinnanie Shale. Thus some of his material is reported as from the upper Wandagee on locality information at the University of Western Australia when it is actually from the lower Wandagee Formation as defined by Condon (1967) (see Material section under *Occiducrinus australis* and *Skaiocrinus granulosus* (herein; Webster,1990).

There has also been some confusion about the locality. Webster (1990), in citing locality data from the University of Western Australia, listed the locality as east of Coolkilya Pool. Teichert (pers. comm. 1990 to GDW) corrected this to west of Coolkilya Pool as shown on the Winning Pool-Minilya 1:250 000 Geological map (sheet SG50-13, 49-16, 1984). When we stopped at Wandagee Homestead the directions we received to Coolkilya Pool took us further west than the location shown on maps. It is obvious, when on the site, that the size and location of the pool or pools along the river bed shift with scour and fill during major runoff and evaporation and infiltration during subsequent dry seasons. Coolkilya Pool as designated on the map and as referred to by the locals are not the same. Teichert apparently used the local designation in his original field locations and recognized they differed when trying to reconcile the Bureau of Mineral Resources map locations.

In the base of the Wandagee Formation as defined by Condon (1967) *Occiducrinus australis, Eoindocrinus praecontignatus, Calceolispongia abundans*, and *Neocamptocrinus* sp. occur along the same bedding surface. *Tapinocrinus spinosus, Skaiocrinus granulosus* and *Jimbacrinus minilyaensis* occur at or close to the same horizon. *Stomiocrinus ferruginus* may also be from the equivalent horizon along the Lyndon River to the north. Several species of *Calceolispongia* occur at higher levels in the Wandagee Formation as described by Teichert (1949).

AGE AND CORRELATION

Discussion of the age and correlation of the Callythara Formation at its type section was given by Webster (1987). We accept the late Sakmarian age for the base of the Callytharra Formation based on ammonoids (Glenister & Furnish, 1961). New taxa reported herein do not alter Webster's (1987) interpretation that the crinoids suggest a slightly younger age of early Artinskian for the Callytharra Formation. The Sakmarian-Artinskian boundary may be within the lower part of the Callytharra Formation.

Notiocatillocrinus callytharraensis, Synbathocrinus constrictus, Neoplatycrinus callytharraensis and *Neocamptocrinus* sp. in the Callytharra Formation throughout the Carnarvon Basin suggests a similar age for the unit over this extent. Correlation of the Callytharra Formation with the Fossil Cliffs Formation of the Perth Basin, and Nura Nura Member of the Poole Sandstone in the Canning Basin were discussed by Teichert (1951) and Condon (1967). Webster (1987) discussed the crinoid correlation of the Callytharra Formation with that of eastern Australian faunas reported by McKellar (1969) and Willink (1978). The late Sakmarian-early Artinskian limestone interval in the basins of Western Australia, in the Oxtrack Formation in Queensland, and the Berriedale Limestone and limestone in the Crinoidal Zone of Tasmania represent a major sea level rise and change to warmer conditions in the Australian part of the Tethyan equivalent to the Sterlitamak and possibly Birshevian cycles (Ross & Ross,1985).

Correlation with the Permian crinoids of Timor remains somewhat of a problem. The crinoid bearing Maubisse Formation limestones of northern Timor were interpreted as reefs and thought to have been thrust onto the autochthonous non-crinoidal Permian strata of southern Timor (Audley-Charles,1965,1968). He considered the Timor Permian deposits to have formed in a trough to the northwest of Australia. Charlton (1989) suggested that the northern part of Timor was allochthonous but thought much of the struc-

FIG. 1. Coelocrinid indet. QMF21428. A, lateral view showing set of arms with distal part of spinose anal tube at upper right, ×1. B, incurved distal parts of flattened arms and spinose anal tube, ×1.6.

tural complexity was best explained by wrench faulting , not by vertical movements as postulated by Chamalaun and Grady (1978). All of these interpretations agree that the Permian deposits of Timor were formed in and along the distal side of a trough that was part of the Australian block as proposed by Hamilton (1979).

The crinoid bearing Maubisse Formation would have been the most distal deposits, an unknown distance, but perhaps as much as 1000km northwest of the Canning and Carnarvon Basins. Plate reconstructions of the Permian (Zonenshain, Kuzim and Kononov, 1985, among others) position Australia along the eastern part of Gondwanaland. The Carnarvon and Canning Basins would have been between 50° S and 40°S. Timor would have been at approximately 25°–30°S. The Timor faunas were considered Late Permian on reports of fusulinids at Amarassi (Schubert,1915) and cephalopods at Basleo (Wanner,1931; Gerth,1950). Haniel (1915) interpreted the cephalopods as middle Permian, on the Early to Late Permian boundary. Brachiopods (Broili,1916) and corals (Gerth, 1921) indicated a Permian age but did not specify Early or Late, whereas C. Wanner (1922) placed an Early Permian age on the gastropods and bivalves. The echinoderms were interpreted as Carboniferous (Bather, 1914; Springer,1920, 1924), in contrast to middle Permian (Wanner, 1924a) and Late Permian (Wanner, 1931).

The lack of stratigraphic control of the numerous crinoid and blastoid localities from Timor has been recognized for many years (Audley Charles, 1965; Glenister & Furnish,1987; among others). Some cephalopod reports with and without stratigraphic control at a few localities include Sakmarian from Somohole, Artinskian from Bitauni, and Late Permian from Amarassi and Basleo (Glenister & Furnish,1987). Grant (1976) considered the Bitauni brachiopods to be of Artinskian age. Sections with stratigraphic control have yielded brachiopods from the Chiddruan Maubisse Formation near Kasliu Village, West Timor (Archbold & Bird,1989) and from the late Sakmarian Khali and Bisnain Members of the Maubisse Formation near Bisnain Village, West Timor (Archbold & Barkham, 1989). The Bisnain brachiopods were correlated with the Callythara Formation by Archbold & Barkham (1989). Artinskian conodonts were recovered from matrix materials and *in situ* limestone blocks collected on early expeditions to Timor (Boogaard, 1987). Thus Timor Permian strata is thought to range from Sakmarian to Amarassian age. Wanner (1931) reported that 90% of Timor crinoids and 75% of all other Permian fossils of Timor are from the Basleo area. It is the age of the Basleo fossils which we consider to be the most problematic because a Late Permian cephalopod has been reported by Glenister and Furnish (1987) from the area. The stratigraphic relationship of the cephalopod and crinoids is unknown.

International correlation based on the crinoids and blastoids suggests an Early Permian age, probably Artinskian or Roadian for the Basleo echinoderms. The Basleo crinoids and blastoids correlate best with Artinskian faunas from the Callythara Formation (12 of the same genera, 3 species; 2 species with affinities and 3 genera with close affinities to Timor genera), the Wandagee Formation (4 of the same genera, 1 species) and the Sarginsk Horizon of the Urals (15 genera). There are few genera and no species in common with the Early Permian of Texas (3 genera), Nevada (7 genera), and Bolivia (2 genus). Few genera and no species are common to the Upper Permian of Russia (1 genus), Sicily (5 genera), Western Australia (1 genus), and eastern Australia (2 genera). These data have been compiled from crinoid occurrences indexed in Bassler & Moody (1943), Webster (1973, 1977, 1986, 1988), and unpublished data.

Until the structure and stratigraphy of the Basleo area are fully understood we consider the echinoderm fauna to be Early Permian recognizing that part of the fauna could be Late Permian based on the cephalopod reported by Glenister & Furnish (1987).

SYSTEMATIC PALAEONTOLOGY

Crinoid terminology follows Ubaghs et al. (in Moore & Teichert, 1978), with columnal patterns after Webster (1974). Blastoid terminology is from Beaver et al. (in Moore, 1967).

Material collected by us during July 1991 came from localities entered in the Queensland Museum Locality Register (QML), and is curated in the Queensland Museum Palaeontological Collection (QMF). Other collections referred to are indicated by the following prefixes: Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra (CPC), Museum of Victoria, Melbourne (NMVP); Western Australian Museum, Perth (UWAF) and Department of Geology, University of Western Australia, Perth (UWAF).

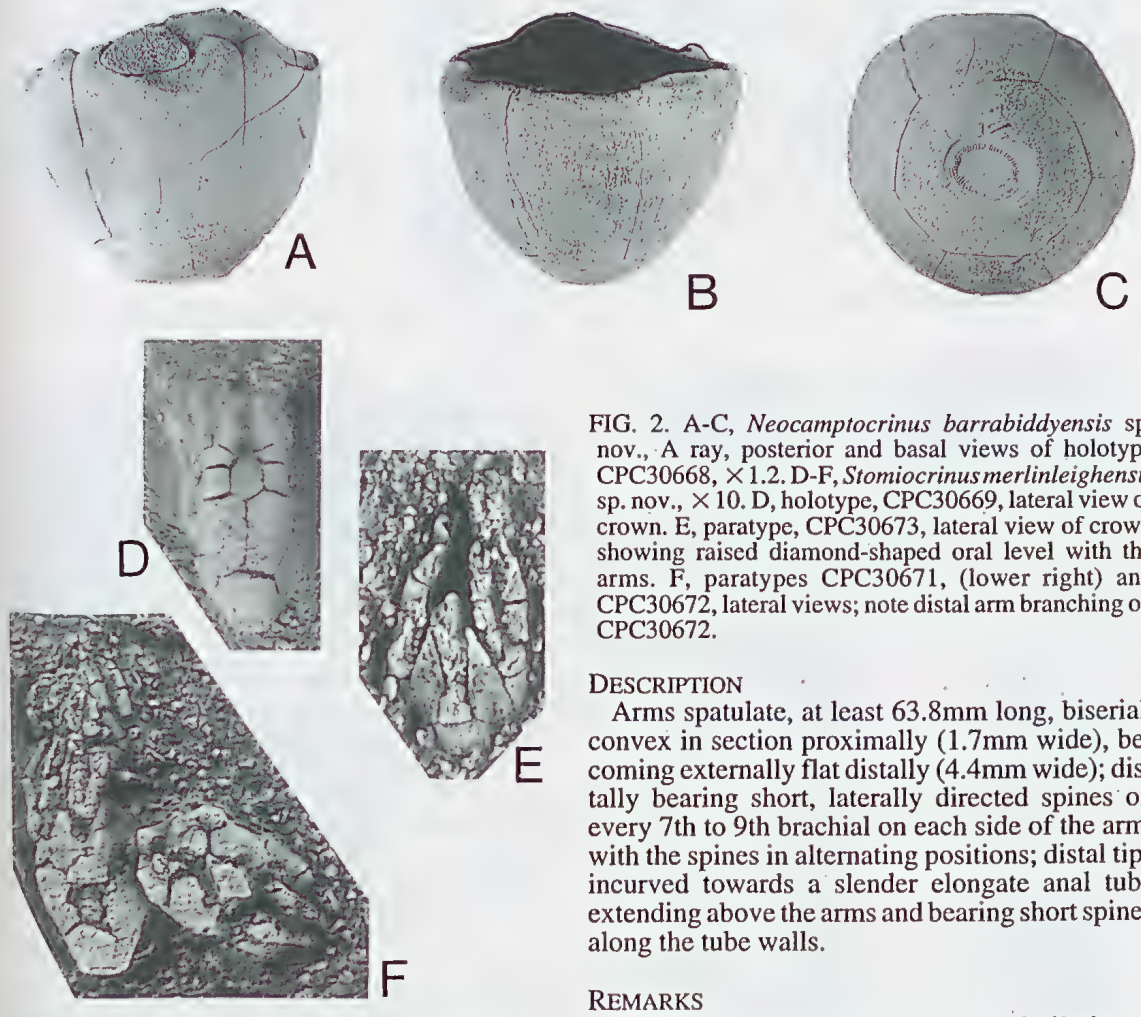


FIG. 2. A-C, *Neocamptocrinus barrabiddyensis* sp. nov., A ray, posterior and basal views of holotype CPC30668, ×1.2. D-F, *Stomiocrinus merlinleighensis* sp. nov., ×10. D, holotype, CPC30669, lateral view of crown. E, paratype, CPC30673, lateral view of crown showing raised diamond-shaped oral level with the arms. F, paratypes CPC30671, (lower right) and CPC30672, lateral views; note distal arm branching on CPC30672.

Subclass CAMERATA Wachsmuth & Springer, 1885
Order MONOBATHRIDA Moore & Laudon, 1943
Suborder COMPSOCRININA Ubaghs, 1978
Superfamily CARPOCRINOIDEA de Koninck & Le Hon, 1854
Family COELOCRINIDAE Bather, 1899

Coelocrinid? indet
(Fig.1)

MATERIAL

QMF21428, a large, weathered, partial set of arms with anal tube, found in three pieces, two of which fitted together, from the middle Callytharra Formation in the eastern line of the Gooch Range south of Carnarvon-Williambury Station road, GR922549 Gooch Range 1: 100,000 topographical sheet (no. 1850), 1974 edition.

DESCRIPTION

Arms spatulate, at least 63.8mm long, biserial, convex in section proximally (1.7mm wide), becoming externally flat distally (4.4mm wide); distally bearing short, laterally directed spines on every 7th to 9th brachial on each side of the arm, with the spines in alternating positions; distal tips incurved towards a slender elongate anal tube extending above the arms and bearing short spines along the tube walls.

REMARKS

This specimen bears remarkable similarity to the illustration (Wachsmuth & Springer, 1897, pl. 42, fig. 5) of *Dorycrinus cornigerus* (Hall, 1858). Anal tube spines of *D. cornigerus* are longer, extending beyond the arms when enclosed. Long spatulate arms are known in several genera of the Batocrinidae and Coelocrinidae (Wachsmuth & Springer, 1897); however, only those of *D. cornigerus* have short laterally directed spines along the sides of the arms. Thus we questionably refer the specimen to the Coelocrinidae.

This is the first Permian report of the otherwise Middle Devonian to Early Mississippian European and North American family (Moore & Teichert, 1978). Other camerates, such as *Actinocrinites*, *Pleurocrinus* and *Camptocrinus*, initially restricted to Early Carboniferous strata of Europe and North America were discovered in the Permian of Timor (Wanner, 1916, 1924a). Thus,

a possible coelocrinid in the Permian of Western Australia adds to the list of camerate holdovers lacking a Late Carboniferous record.

Superfamily HEXACRINITOIDEA Wachsmuth & Springer, 1885

Family DICHOCRINIDAE Miller, 1889

Subfamily CAMPTOCRININAE Broadhead, 1981

Neocamptocrinus Willink, 1980

TYPE SPECIES

Neocamptocrinus bundanoonensis Willink,1980, from the Kazanian Berry Formation, New South Wales; by original designation.

REMARKS

Willink (1980) recognised *Neocamptocrinus* on the inflated tegmen and a column that is elliptical throughout its length instead of round adjacent to the cup as is *Camptocrinus*. Carboniferous and Permian camptocrinid columns show that the elliptical shape is similar in both, that is nearly round, but definitely slightly elliptical, adjacent to the cup becoming progressively elliptical in a few centimetres distally and remaining elliptical throughout the remainder of the known column. The long axis of the columnal attains its greatest size in the Permian of Western Australia (Fig. 3M,N). Cups assigned by Willink (1980), Webster, (1990) and herein show an evolutionary and stratigraphic record of potential value for the Permian of Australia and Timor. We question the degree of inflation of the tegmen as a generic feature; however, for convenience we apply the name to these Permian forms including *Camptocrinus* cf. *C. indoaust-ralicus* Wanner (Webster,1987:102, fig. 5J-M).

Columnals of *Neocamptocrinus* are common in many parts of the Permian of Western Australia (Webster, 1987, 1990; herein). Even proximal, nearly circular columnals are easily recognised by the distinctive, off centre, axial canal and unequal length of culmina on the opposing long sides of the articulum. Additional study of *Neocamptocrinus* columnals in Western Australia is necessary to determine their strat-igraphic value. Columnals of *Neocamptocrinus* sp. are present in the Callytharra Formation at all localities we collected. No cups were found, but the radials listed as indeterminate camerate radial 4 and 5 by Webster (1987) probably belong to a new species of *Neocamptocrinus*.

Neocamptocrinus barrabiddyensis sp. nov. (Fig. 2A-C)

ETYMOLOGY

For Barrabiddy Creek.

MATERIAL

Holotype CPC30668, Bulgadoo Shale, east limb of Barrabiddy Anticline, Barrabiddy Paddock, 1/4 mile south of mill.

DIAGNOSIS

Radial notches relatively narrow; radials more expansive.

DESCRIPTION

Cup bowl-shaped, wider (29.1mm) than high (21.8mm), base truncated, widest at base of radial facets, sutures flush, no ornamentation. BB 2, suture faint, 5.6mm wide, 5.5mm high, upflared, slightly concave walls. RR 5, longer (19.4mm) than wide (16.0mm), gently convex transversely, convexo-concave longitudinally. Radial facets angustary, c. 2/3 radial width; transverse ridge elevated, with coarse ridges normal to ridge length; brachial canal circular in section; muscle fields elliptical, long axis subparallel to transverse ridge, moderately impressed; ambulacral groove narrow, sloping inward. Anal longer (19.6mm) than wide (11.3mm), narrower than and in line with radials. Columnal facet elliptical, 8.7mm long, 63mm wide, impressed; articulum narrow; culmen coarse, cog-like, areola wide, flat. Stem and arms unknown.

REMARKS

This robust cup was weathered out of red claystone containing abundant disarticulated plates of *Calceolispongia* cf. *barrabiddyensis*. It has narrower radial notches, radials that distally expand transversely at a greater rate and lower radial facets than *N. occidentalis* Webster, 1987 or *N. millyitensis* sp. nov. These two species probably evolved from *N. barrabiddyensis*.

Neocamptocrinus millyitensis sp. nov. (Fig. 3A-L)

Neocamptocrinus sp. nov. Webster, 1990:57, pl. 1, figs 7-11.

ETYMOLOGY

For the Millyit Range.

MATERIAL

Holotype CPC27054, paratypes CPC27455-27457 from the Millyit Range. Other material, QMF21420-

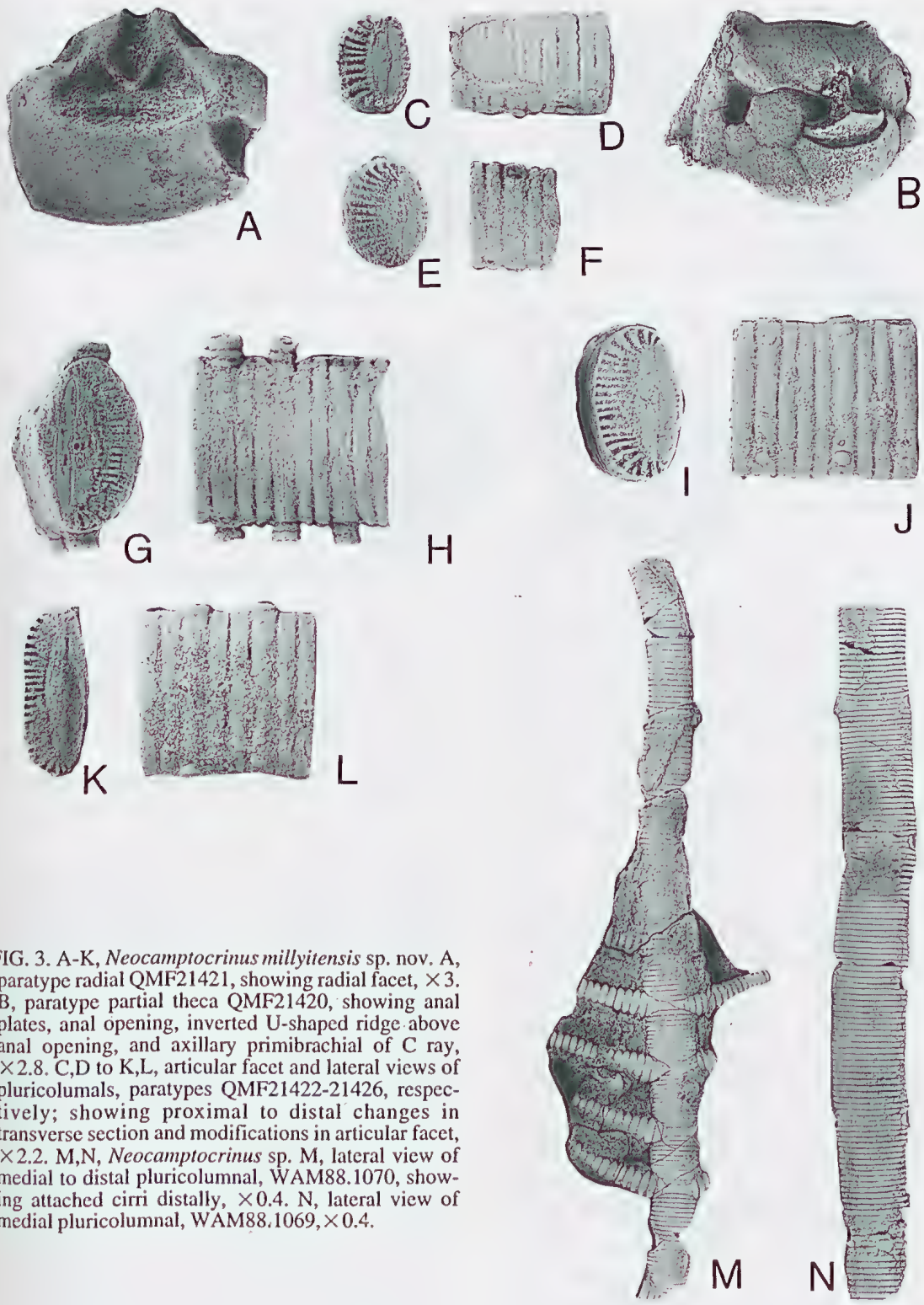


FIG. 3. A-K, *Neocamptocrinus millyitensis* sp. nov. A, paratype radial QMF21421, showing radial facet, ×3. B, paratype partial theca QMF21420, showing anal plates, anal opening, inverted U-shaped ridge above anal opening, and axillary primibrachial of C ray, ×2.8. C,D to K,L, articular facet and lateral views of pluricolumals, paratypes QMF21422-21426, respectively; showing proximal to distal changes in transverse section and modifications in articular facet, ×2.2. M,N, *Neocamptocrinus* sp. M, lateral view of medial to distal pluricolumnal, WAM88.1070, showing attached cirri distally, ×0.4. N, lateral view of medial pluricolumnal, WAM88.1069, ×0.4.

21426 from QML772,Millyit Range, Canning Basin from the Cherrabun Member, Hardman Formation,

DESCRIPTION

See Webster, 1990:57.

REMARKS

Webster (1990) left material available at that time in open nomenclature because its precise locality and horizon were unknown. We have now collected further material from a well-defined locality and horizon, which may well be the type locality.

The partial theca shows 3 anal plates, with a large primanal in the radial circlet, a small anal opening above the central anal plate and an inverted V-shaped ridge on the overlying oral. Both orals bear a coarse central node. Radial facet has a transverse ridge with a parallel shallow outer ligament pit, two shallow muscle fields and a T-shaped ambulacral track aborally.

Pluricolumnals are mostly short segments but show the change in sectional shape from nearly circular proximally to distally elliptical. The articular facet of the proximal columnals has long coarse culmina on the upper side of the columnal and very short culmina on the under side. Culmina become coarser laterally on the facet. The areola is higher on the upper side with faint traces of culmina across the surface. On the underside, the areola is smooth and half the width of that on the upper side. Axial canal is small and round.

Neocamptocrinus sp.
(Fig. 3M,N)

MATERIAL

Pluricolumnals WAM88.1069-88.1070 from north bank, Minilya River in the fourth massive sandstone of the Wandagee Formation, Coolkilya Pool area, Wandagee Station. Collected K.J. McNamara.

REMARKS

These are the longest articulated pluricolumnals of *Neocamptocrinus* known from Western Australia. They are 28cm and 28.5cm long with columnals 30mm wide, 9mm thick and 2.2mm high. In a proximal direction noditaxes consisted of 22, 23, 24, and 26 columnals each on WAM88.1069. Cirri are initiated at the junction between two columnals and may grow to extend over the height of four columnals; the axial canal is also shared by the two columnals. Columnal growth after initial growth of the cirrus extends beyond the distal edge of the proximal cirral to partly cover the proximal end of the second cirral. Cirri are round in section. Crenularium 1.8mm wide, slightly less than half cirral radius (4.1mm); culmina fine. Areola planar. Axial canal small and round. Cirri taper distally with semipointed ends. These large columnals lack the more rounded proximal and distal sections of the stem. They show that considerable lengths of the stem acted as a runner with the cirri extended out and down into the substrate. It is unknown if the flexures in the two stem sections reflect flexibility around substrate irregularities or diagenetic distortion.

Stomiocrinus Wanner, 1937

TYPE SPECIES

Stomiocrinus subglobosus Wanner, 1937 from the Permian of Timor; by original designation.

Stomiocrinus merlinleighensis sp. nov.
(Fig. 2D-F)

ETYMOLOGY

For the Merlinleigh Subbasin, Carnarvon Basin.

MATERIAL

Holotype CPC30669, paratypes CPC30670-30676 from micaceous limestone in the top of the Bulgadoo Shale, at type locality, near Donnelly's Well.

DIAGNOSIS

Orals elongate, steeply upflared, visible in lateral view.

DESCRIPTION

Crown small, cylindrical. Cup bullet-shaped, widest at radial summit, fine shagreen ornamentation. BB 2, equidimensional, forming lower 1/3 of cup, upflared steeply; interbasal suture in plane of symmetry. RR 5, longer than wide, outflaring gently longitudinally, moderately convex transversely, straight to slightly convex longitudinally. Radial facets angustary, approximately 1/3 greatest radial width, subhorizontal. Brachials rectilinear, longer than wide, strongly convex transversely, straight longitudinally; IBr2 or 3 axillary; one additional branching in some rays; all branchings isotomous. No pinnules. Anal in radial circlet, slightly narrower than radials. OO 5, elongate, steeply upflared, raised medial section flush to slightly inset to proximal brachials, mutual lateral edges underlay proximal brachials and form base of ambulacral groove from the base of the arms to the mouth. Posterior oral largest.

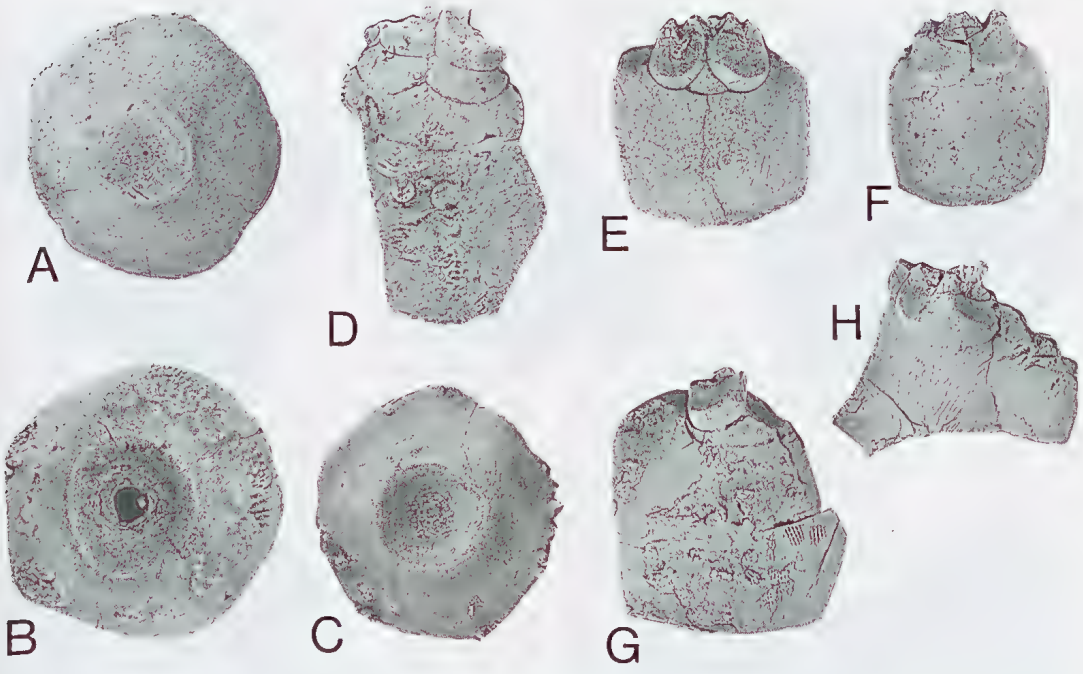


FIG. 4. *Neoplatycrinus callytharraensis* sp. nov. all from QML757, ×1. A-C, basal circlets QMF21594, 21593, and 21592, respectively. D–H, radials with primibrachs and in some cases secundibrachs attached, QMF21595, 21599, 21597, 21598, and 21596, respectively.

MEASUREMENTS (mm)

	Holotype	Paratype
Crown length	3.6 (incomplete)	3.3
Crown width	1.5	1.2
Cup length	1.6	1.2
Cup width	1.3	1.1
Basal circlet diameter	0.7	0.7
Basal circlet length	0.6	0.6
Radial length	1.0	0.8
Radial width	0.8	0.7

REMARKS

Stomiocrinus is reported from the Permian of Timor, Russia (Broadhead, 1981) and Western Australia (Webster, 1990). Broadhead (1981) assigned *Stomiocrinus* to the Camptocrininae based on Yakovlev's (in Yakovlev & Ivanov, 1956) combination of disassociated thecae and bilaterally symmetrical columnals. The crowns of *S. merlinleighensis* occur on three small blocks associated with *Jimbacrinus donnellyensis* and *Calceolispongia acuminata*. None of the crowns of *S. merlinleighensis* has the stem attached whereas the crowns of *J. donnellyensis* have the proximal stem attached. It is unknown if the proximal stem of *C. acuminata* is attached.

In the matrix there are numerous thin round pluricolumnals which contain columnals of 4mm diameter and 7mm length that might have been the stem of *S. merlinleighensis*. They differ from the short cirral segments (7mm diameter, 2mm long) which are articulated with the attached stems on *J. donnellyensis*. There are no bilaterally symmetrical columnals in the matrix. This leaves the subfamily affinity of *Stomiocrinus* in doubt until articulated thecae and columnals are found.

Superfamily PLATYCRINITOIDEA Austin & Austin, 1842

Family PLATYCRINITIDAE Austin & Austin, 1842

Neoplatycrinus Wanner, 1916

TYPE SPECIES

Neoplatycrinus dilatatus Wanner, 1916, from the Permian of Timor; by original designation.

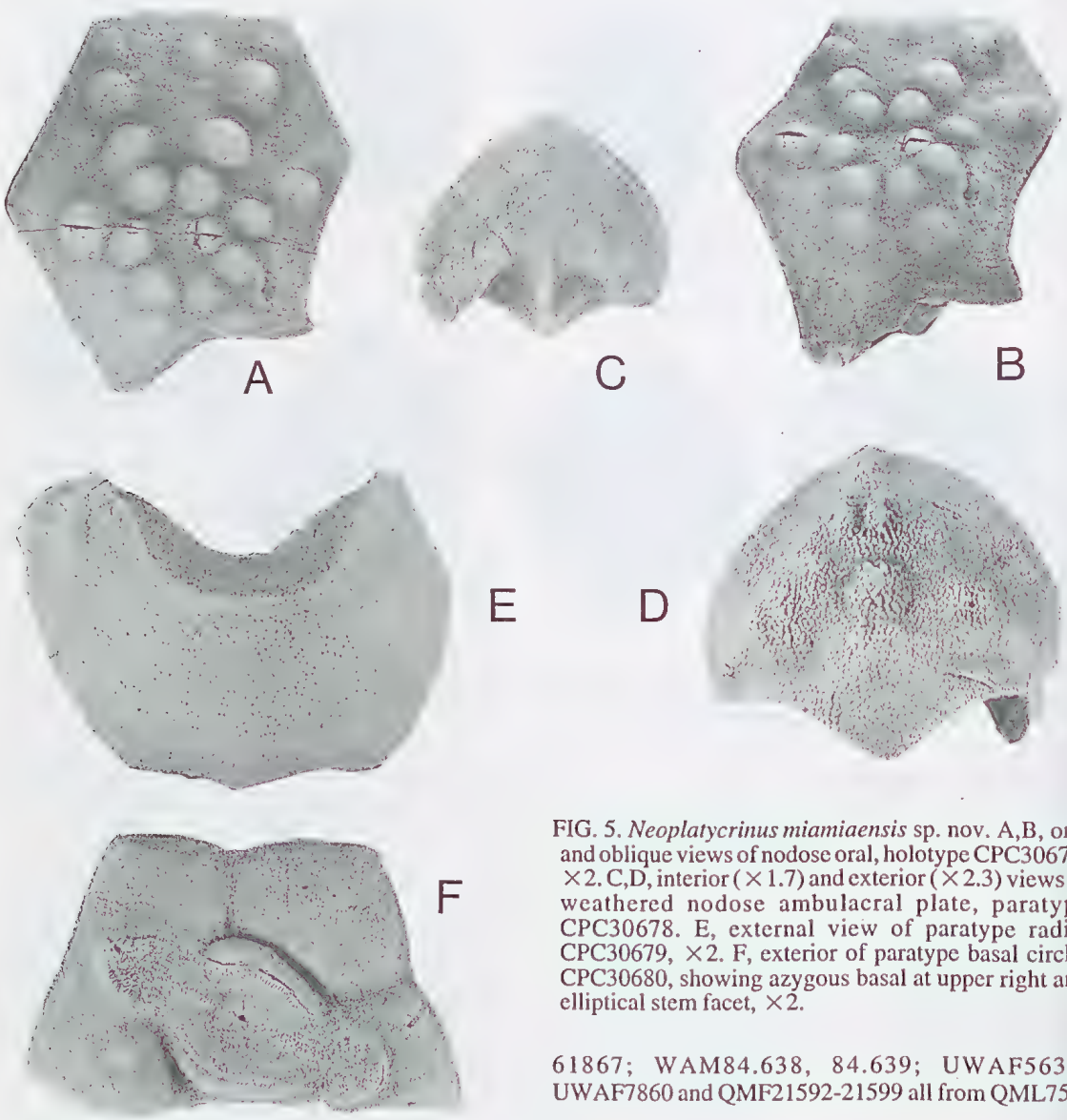


FIG. 5. *Neoplatycrinus miamiaensis* sp. nov. A,B, oral and oblique views of nodose oral, holotype CPC30677, ×2. C,D, interior (×1.7) and exterior (×2.3) views of weathered nodose ambulacral plate, paratype CPC30678. E, external view of paratype radial CPC30679, ×2. F, exterior of paratype basal circlet CPC30680, showing azygous basal at upper right and elliptical stem facet, ×2.

Neoplatycrinus callytharraensis sp. nov. (Fig.4)

Neoplatycrinus aff. *N. somoholensis* Wanner, 1916; Webster, 1987:100, figs 4A-O.
Pleurocrinus? sp. Webster, 1987:101, fig. 4P,Q.

ETYMOLOGY
For Callytharra Springs.

MATERIAL
Holotype UMMP61862. Paratypes UMMP61863-61867; WAM84.638, 84.639; UWAF5638, UWAF7860 and QMF21592-21599 all from QML757.

DIAGNOSIS
Oral and ambulacral plates with large node or coarse ridges.

DESCRIPTION
As given by Webster, 1987, p. 100-101.

REMARKS
This species is based on disarticulated oral and ambulacral plates bearing one very large node and secondary smaller nodes or very coarse discontinuous ridges. Basal and radial plates assigned lack these coarse nodes as is the case in *N.*

miamiaensis, described below. We found the ornamented orals and ambulacral plates disassociated in proximity to the unornamented basal circlets and radials.

Webster, 1987, referred the Callytharra Formation specimens to *N.* aff. *N. somoholensis*, a species based on internal molds (Wanner, 1916, 1924a). The ambulacral plates of *N. somoholensis* are divided distally by a deep V-shaped separation (Wanner, 1924a, pl. 3, fig. 2). Division on the ambulacral plates of *N. callytharrensis* is not as deep (Webster, 1987, fig. 4A). The upper distal part of oral plates of *N. somoholensis* would overhang the proximal vertical section whereas they do not on *N. callytharraensis*. All other described species of *Neoplatycrinus* lack ornamentation on the oral and ambulacral plates.

Neoplatycrinus miamiaensis sp. nov.
(Fig. 5)

ETYMOLOGY

For Mia Mia Station.

MATERIAL

Holotype CPC30677, paratypes CPC30678-30681 all from the lowermost fossiliferous horizon in the Artinskian Coyrie Formation, east of Mia Mia Homestead, 23°21'S, 114°34'E, northern Carnarvon Basin. Other material CPC30711-307153, a columnal, 2 radials and 2 tegmen plates from the lower part of the Noonkanbah Formation at the type section (BMR loc. KNF73), Canning Basin.

DIAGNOSIS

Basal circlet subhorizontal; orals and ambulacrals bearing coarse nodes in radiating to irregular patterns.

DESCRIPTION

Basal circlet large, estimated 32mm diameter, subhorizontal; bears elliptical stem facet, 2.3mm long, 9.3mm wide. BB 3, 2 large, 1 small (16mm long, 15.5mm wide) surface coarsely granulate, with coarse node (2.8mm diameter) on one plate. RR 5, wider (28.4mm) than long (20.7mm), convex longitudinally and transversely, surface with coarse granules, no nodes. Radial facet wide, 2/3 plate width, narrow, crescent shaped. OO 5, large, estimated 35mm long, 28.2mm wide, polygonal, proximally vertical, distally subhorizontal or upflared, with 8 to 18 coarse nodes (4.4mm diameter, 2.8mm high) in radiating or irregular pattern and coarse granular ornament. Proximal ambulacral quadrangular, 18.9mm long, 19.3mm wide, sharply pointed proximally and distally, side vertical, exterior with up to 9 coarse nodes and coarse granular ornamentation.

REMARKS

The description is based on disarticulated ossicles from one horizon in the Coyrie Formation. The theca is estimated to have been up to 75mm wide and 45mm high, with a low bowl shape having a flat base, low out-flared radials, and a broad flat to upflared tegmen. Interpretation of the theca is based on: 1, a flat wide basal circlet (Fig. 5F); 2, radials attached to the vertical facets on the basal circlet such that the proximal end of the radial was horizontal, expanding the low bowl laterally; 3, radials are convex longitudinally resulting in the distal parts of the radial being essentially vertical; the radial facet would have sloped down and out at an estimated 80°; and 4, the proximal end of the orals was probably nearly vertical and the distal part subhorizontal to upflared perhaps as much as 40°. Mutual facets on the radials and orals are not well preserved precluding firm estimate of reconstruction.

Secundibrachials associated with the thecal plates bear the same coarse nodes and granulate ornamentation. They are U-shaped with two deep V-shaped ambulacral grooves, one large and one smaller and lateral. Most plates show growth bands on the aboral side. Solution weathering has modified the surfaces of most plates, removing or obliterating the granular ornament is common, and in extreme examples nodes are reduced to small stellate elevations. Diagenetic distortion and fracturing followed by calcite cementation sealing the fractures is present on some plates.

Numerous internodals and nodals of the "twist" nodal columnals were found in association with the thecal plates. They are assigned to the species because all other crinoids in the fauna are non platycrinitids. No difference could be discerned between these columnals and ones found in the Callytharra Formation. This suggests that mosaic evolution was occurring in the theca while the columns were stable.

Neoplatycrinus is restricted to the Permian of Timor (Lane in Moore & Teichert, 1978) and Western Australia (Webster, 1987). The genus is recognized by the large oral plates. *N. miamiaensis* is distinguished from *N. callytharraensis* by its oral and ambulacral plate ornamentation. It differs from *N. somoholensis* by having a flat base instead of being upflared at 30° to 40°. Evolution of *N. miamiaensis* from *N. callytharraensis* occurred by modification of oral and ambulacral ornament.

The original field label on specimens of *N.*

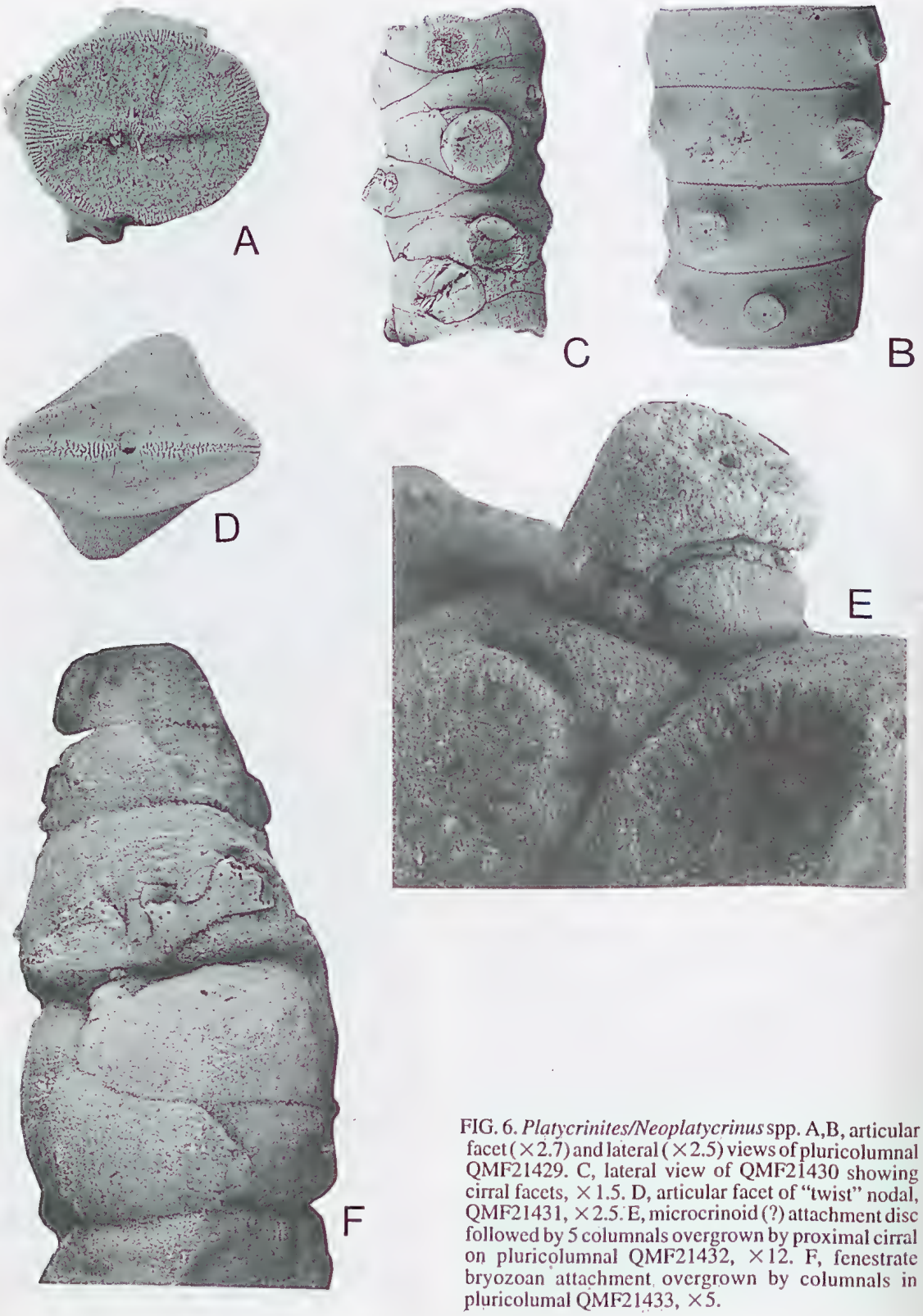


FIG. 6. *Platycrinites/Neoplatycrinus* spp. A,B, articular facet (×2.7) and lateral (×2.5) views of pluricolumnal QMF21429. C, lateral view of QMF21430 showing cirral facets, ×1.5. D, articular facet of "twist" nodal, QMF21431, ×2.5. E, microcrinoid (?) attachment disc followed by 5 columnals overgrown by proximal cirral on pluricolumnal QMF21432, ×12. F, fenestrate bryozoan attachment overgrown by columnals in pluricolumal QMF21433, ×5.

miamiaensis gave the stratigraphic unit as the Bulgadoo Shale. However the latitudinal coordinates place the locality in the Coyrie Formation as mapped on the Winning Pool-Minilya 1:250,000 Geological Sheet SF50-13, 1984.

The columnal, radials and tegmen plates from the Canning Basin bear the same ornamentation on the oral and brachial as described above.

Platycrinites/Neoplatycrinus spp.
(Fig. 6)

MATERIAL

Figured material QMF21429,21431 from QML760, QMF21430, 21432, 21433 from QML757 and other material 181 internodals, 102 nodals and 39 pluricolumnals QMF21578 (203) from QML757, QMF21579 (26) from QML758, QMF21580 (14) from QML759, QMF21581 (13) from QML760, QMF21582 (9) from QML761, QMF21583 (19) from QML758-761, QMF21584 (18) from QML769 and QMF21585 (6) from QML770.

DESCRIPTION

Internodals elliptical, opposing fulcral ridges parallel; nodals rectangular to subquadrate, opposing fulcral ridges at 15-80° with most 67° or 80°. All columnals wider than high, elliptical axial canal, very fine shagreen ornamentation. Noditaxis variable, 1-5 internodals. Articulum divided in half by prominent fulcral ridge. Fulcral ridge depressed below articular rim adjacent to axial canal, bears transverse vermiform to short medium coarse ridges proximally, 3 to 7 medium coarse slightly radiating culmina distally. Crenularium narrow; culmina short, medium coarse, lengthening near fulcal ridge, producing a fan shaped pattern, unbranched. Areola divided by fulcral ridges, each half crescent in outline, smooth, sloping into shallow trough paralleling fulcral ridge, deepest abaxial of axial canal. Axial canal small, elongate parallel to fulcral ridge. Latus gently to moderately convex on lateral sides, moderately convex to vertical to gently concave on ends of internodals, rarely bears small nodes. May bear cirri in distal most parts of stem.

Cirri round transversely; articulum round. Crenularium 1/3 radius; culmina coarse, cog-like, may branch isotomously once. Areola smooth, flat. Axial canal round.

REMARKS

The elliptical columnals vary from elongate (18.6 x 9.4mm) to subcircular (21.8 x 19.5mm) in adults. The more subcircular specimens are mostly cirral bearing and judged to be more distal columnals, whereas the more elongate elliptical forms lack cirri and are considered to be more proximal. Thickness of individual nodals and internodals is uniform except in the cirral bearing distal stem parts where they show pinching and swelling in lateral view.

Cirral facets occur on nodals or internodals and slant distally 5-10°. They are most commonly developed on one or both ends of the long axis but also occur along the short axis of the facet. There are up to 4 cirri per columnal, with one the most common. First cirrus is wedge shaped with distal facet sloping distally thereby increasing the distal slope of the cirrus. Cirri short, tapering distally.

Most specimens are weathered with loss of surface articulum and axial canal details and enhancement of growth bands. Up to 11-14 growth bands weathered as ridges and grooves. Similar growth bands on large cup plates of *Neoplatycrinus* aff. *N. somoholensis*, *Platycrinites wrighti* and *Pleurocrinus*? sp. were illustrated by Webster (1987). These columnals probably belong to those species and are therefore left in open nomenclature.

Organisms attached to the living column of *Platycrinites/Neoplatycrinus* spp. include bryozoans (Fig.6F) and other crinoids (Fig.6E) as both are found overgrown by columnals or cirri. *Phosphannulus* infestations are rare on *Platycrinites/Neoplatycrinus* spp. Columnals, as postmortem detrital grains were used as attachment sites by various sessile organisms but most commonly bryozoans. Diagenetic compaction distorts the areola of numerous specimens.

Subclass INADUNATA Wachsmuth & Springer, 1885
Order DISPARIDA Moore & Laudon, 1943
Superfamily ALLAGECRINOIDEA Carpenter &Etheridge, 1881
Family ALLAGECRINIDAE Carpenter & Etheridge, 1881

Wrightocrinus Moore, 1940

TYPE SPECIES

Allagecrinus jakovlevi Wanner, 1929 from the Permian of Timor; by original designation.

Wrightocrinus wooramelensis sp. nov.
(Fig. 7A,B, I-K)

ETYMOLOGY

For the Wooramel River.

MATERIAL

Holotype QMF21438 from QML757, paratypes

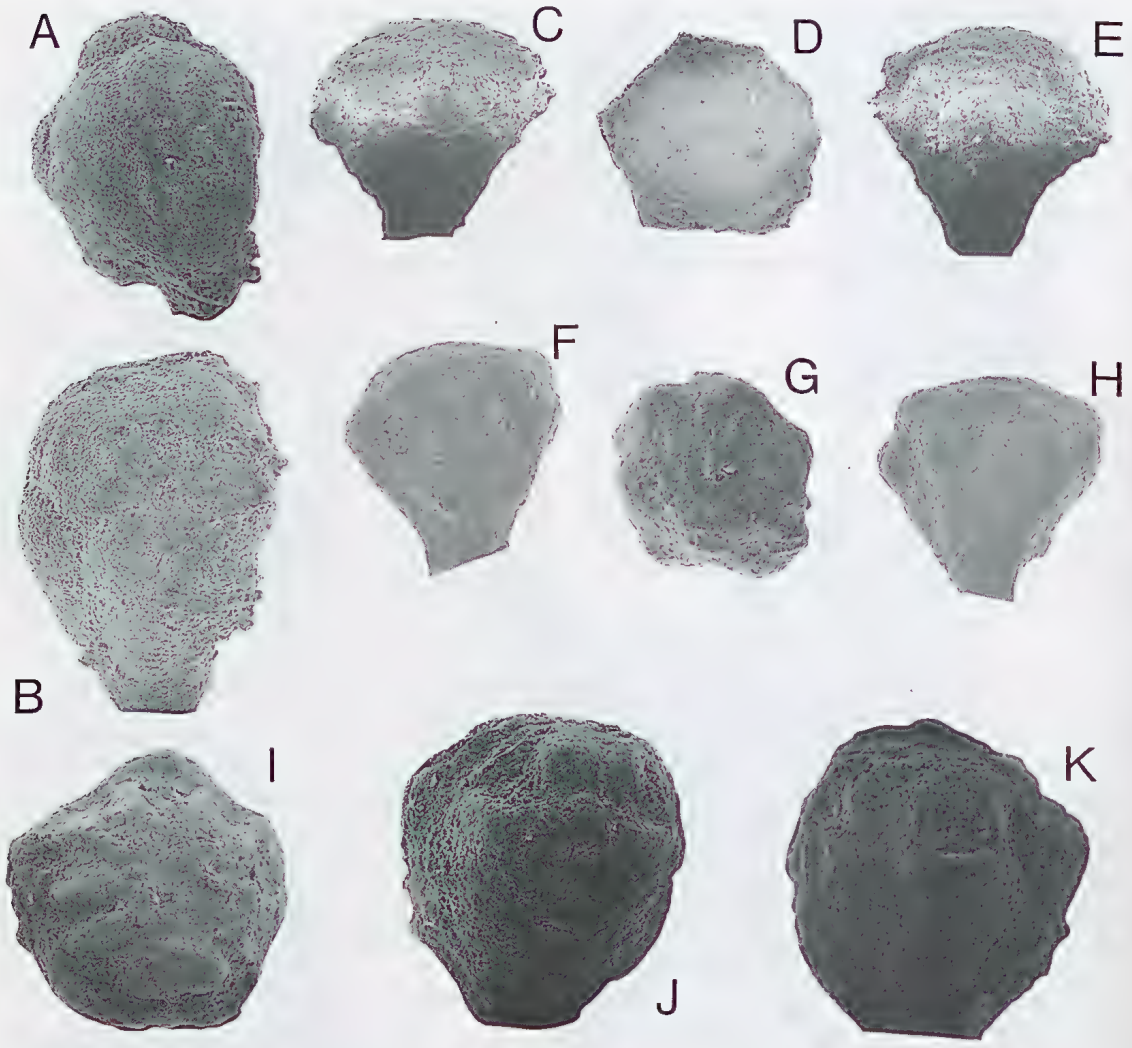


FIG. 7. A,B, I-K, *Wrightocrinus wooramelensis* sp. nov. oral and C ray views of partly crushed paratype QMF21439, A ×30; B ×40. I-K, oral, posterior and A ray views, of holotype QMF21438, ×30. C-H, *Litocrinus pansus* sp. nov. C-E, AB interay, oral and D ray views of holotype QMF21448, ×40. F-H, A ray, oral and posterior views of paratype QMF21449 ×40.

QMF21439 (QML760), CPC30692 (QML757-761) and three crushed thecae QMF21554 (QML759), QMF21555(QML761), all from west of Callytharra Springs.

DIAGNOSIS

Radials protuberent; radial facets narrow; basals short; orals with an elongate central depression.

DESCRIPTION

Theca 1.1mm high, 1.0mm wide, globose, convex walls in lateral view, rounded pentagonal outline in oral view, walls smooth. BB 2, suture slightly rotated off A-CD plane, low, proximally horizontal, bearing round articular facet for stem, distally upturned, flaring outward, forming lower 1/5 of cup. RR 5, 3/4 as wide as long, widest at midlength, outflared proximally, incurved distally, moderately convex longitudinally, transversely gently convex proximally, strongly convex distally, with one facet each; radial facets peneplenary, sloping inward, pit-like. Slight anal notch on mutual shoulders of C and D radials. OO 5, elliptical, slightly longer than wide, central linear depression bordered by rounded low ridge,

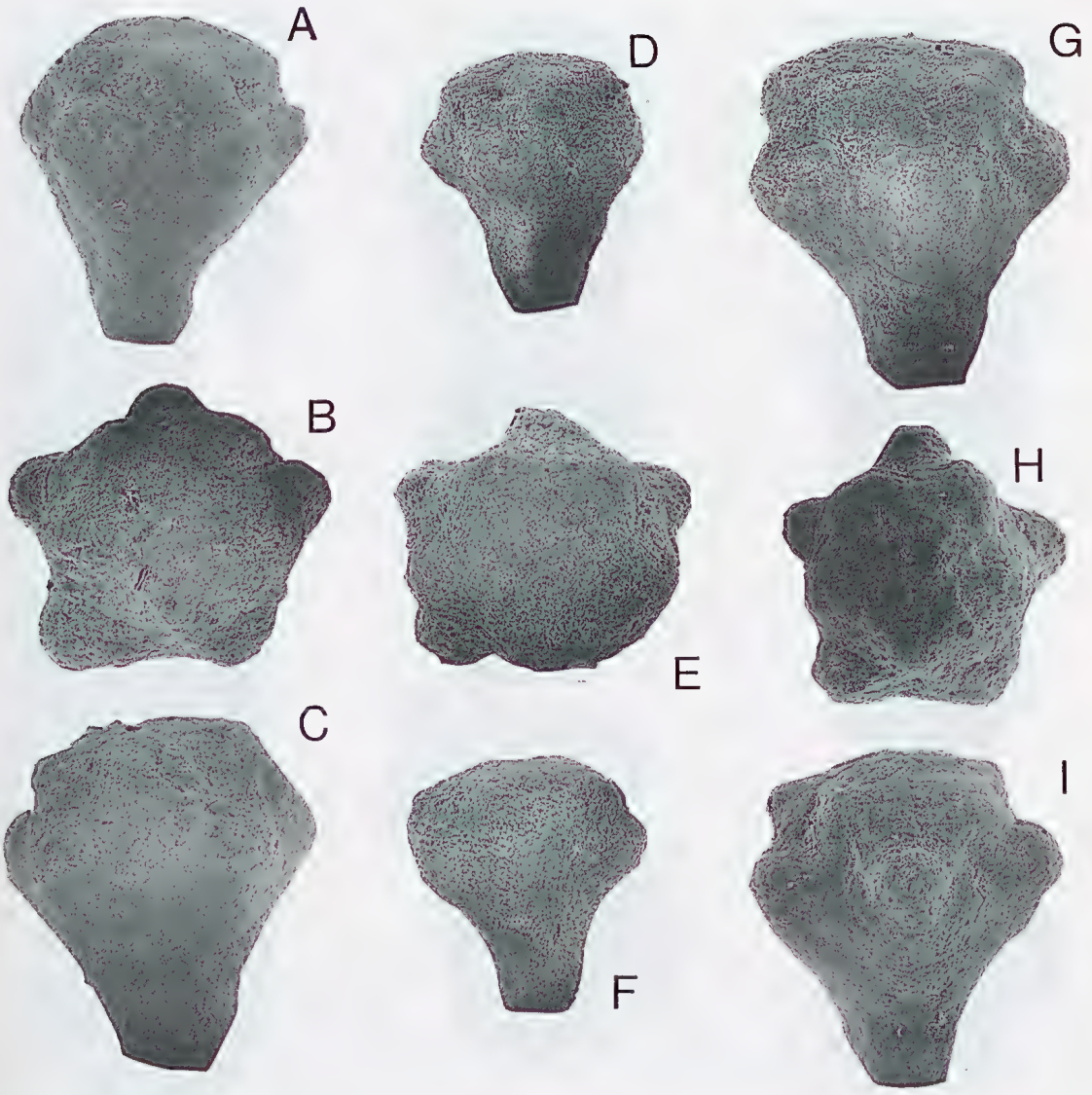


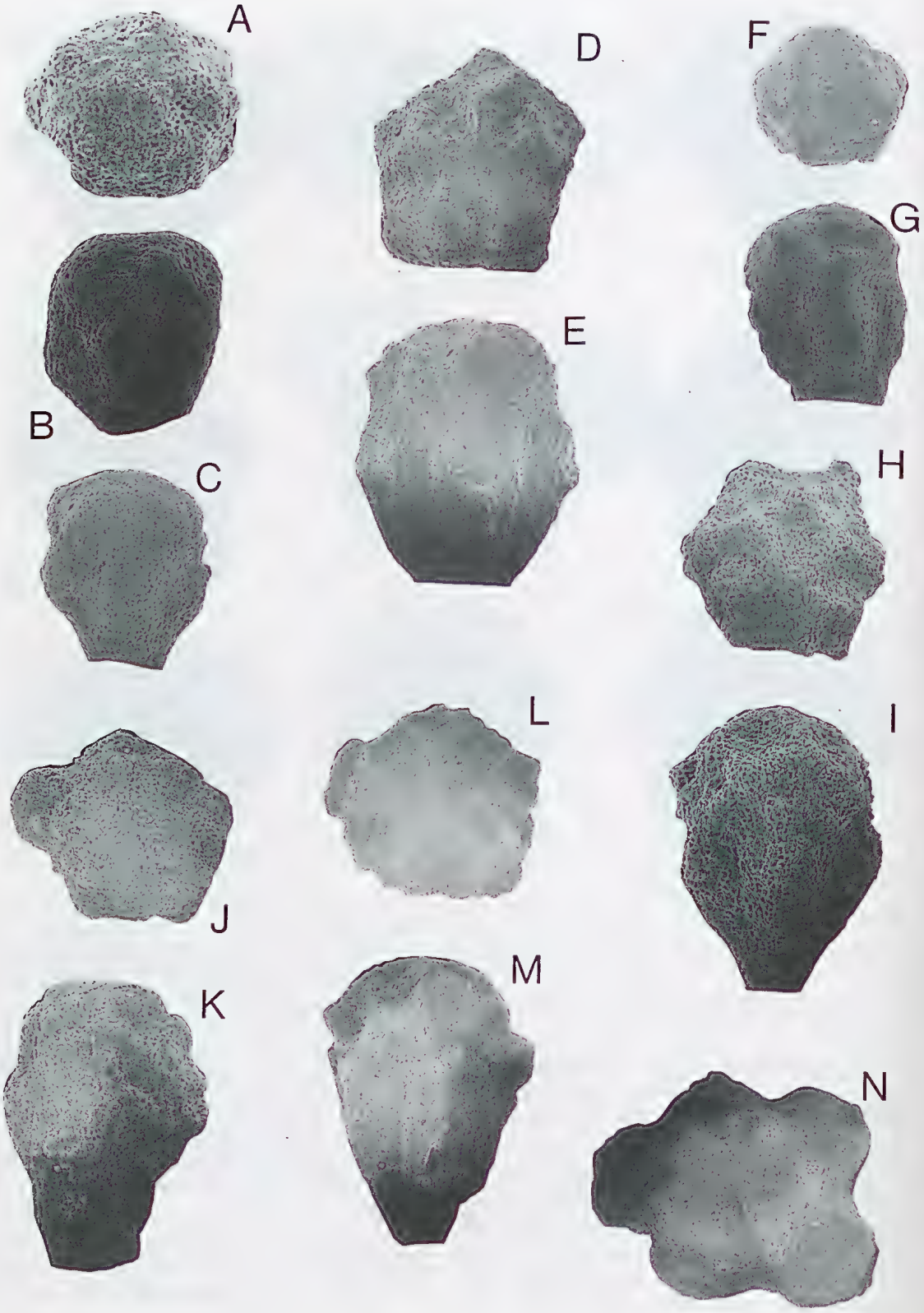
FIG. 8. *Litocrinus protuberans* sp. nov. A-C, BC interray, oral and posterior views of paratype QMF21441, ×40. D-F, A ray, oral and posterior views of paratype QMF21442, D ×40; E ×50; F ×40. G-I, A ray, oral and E ray views of holotype QMF21440, ×40.

form flat-topped elevated circlet slightly inset from radial summit. Posterior basal largest, as wide as long, separating BC and DE orals.

REMARKS

The holotype has a small calcite deposit on the EA oral extending onto the mutual shoulders of the E and A radials. At a cursory glance this falsely appears to be the posterior oral. The posterior oral is recognised by the suture with the other four orals and the small anal notch below it. All specimens of *W. wooramelensis* may be immature, lacking the development of additional arms in the A, C and D rays.

The globose appearance of *W. wooramelensis* is similar to immature specimens of *W. jakovlevi* (Wanner, 1929) but distinguished from it by having more protuberant radials, narrower radial facets, shorter basals and orals bearing an elongate central depression. Webster & Jell, in press, discussed the reasons, essentially that one is a


A
B
C
D
E
F
G
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K
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N

FIG. 10. A-H, *Synbathocrinus constrictus* (Wanner, 1916), initial brachials. A-C, aboral, lateral and brachial facet views, QMF21478, ×25. D-F, brachial facet, lateral and aboral views of QMF21479. A ×25; B,C ×30 . G,H, oral and C ray views of abnormal specimen with only 4 rays and 4 oral plates, QMF21462, ×30. I-M, Microcrinoid holdfasts gen. et sp. indet. I,J, oral and lateral views of rectangular shaped base, QMF21477. I ×25; J ×30. K,L, oral and lateral views of hexagonal base QMF21475, K ×25; L ×30. M, oral view of rectangular base QMF21476, ×30.

FIG. 9. *Synbathocrinus constrictus* (Wanner, 1916). A-C, oral, A ray and E ray views of QMF21461, A ×50; B,C ×40. D,E, oral and B ray views of QMF21464, ×30. F,G, oral and C ray views of abnormal specimen, A and B rays semifused, QMF21467, ×25. H,I, oral and D ray views of pre arm stage QMF21460, ×50. J,K, oral and B ray views of one armed stage, QMF21465, ×30. L,M, oral and A ray views of 2- armed stage, QMF21466, ×20. N, oral view of 4-armed stage, QMF21463, ×20.

juvenile of the other, for placing *Allagecrinus quinquebrachiatus* Wanner, 1929 in synonomy with *W. jakovlevi*.

Litocrinus Lane & Sevastopulo, 1982

TYPE SPECIES
Kallimorphocrinus punctatus Lane & Sevastopulo,1981, from the Lower Carboniferous of Tennessee; by original designation.

Litocrinus pansus sp. nov.
(Fig. 7C-H)

ETYMOLOGY
Latin *pansus*, spread out, extend.

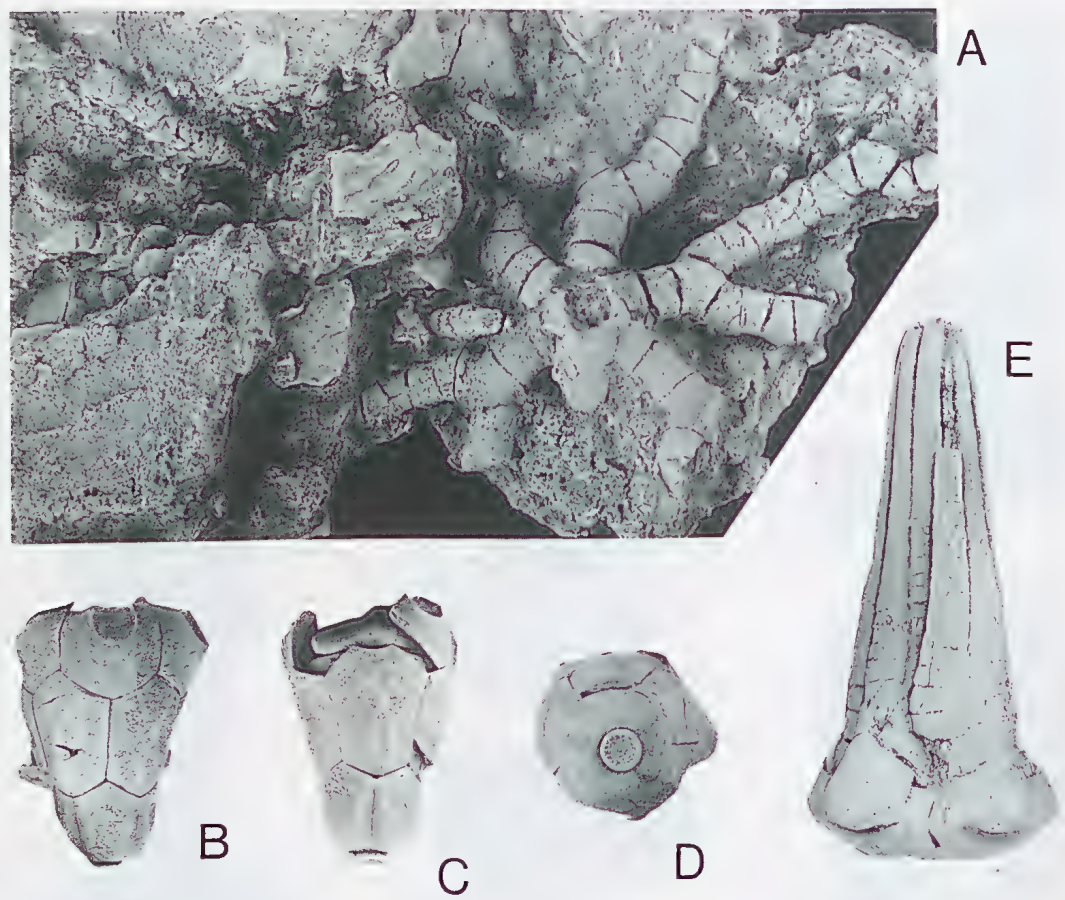


FIG. 11. A, *Spheniscocrinus australis* sp. nov., basal view of holotype, showing base of anal tube in 6 o'clock position on cup, CPC30682, ×3. B-D, *Occiducrinus australis* Webster, 1990, A ray, posterior and basal views of QMF21427, ×1. E, *Tapinocrinus spinosus* (Wanner, 1924a), posterior view showing distal tips of arms, QMF21427, ×1.6.

MATERIAL

Holotype QMF21448 from QML760, paratype QMF21447, 21449 from QML757, QMF21446 from QML759, and other material QMF21556 (1) from QML757, QMF21557 (3) from QML759, QMF21558 (1) from QML760 and QMF21559 from QML761.

DIAGNOSIS

Theca expanded markedly above narrow basal circlet; oral circlet dome-shaped.

DESCRIPTION

Theca small, equidimensional, 0.4-0.6mm, pyriform, walls concave. expanding rapidly above basal circlet, unornamented. BB 5 or fused, small, forming lower 40% of cup, gently outflared. RR 5, longer than wide, moderately convex transversely, concave longitudinally with straight to convex distal ends, may be weakly protruding distally. OO 5, rounded proximal edge in oral view, proximally steeply upflared, distally subhorizontal, may bear weakly elevated protrusion at upflaring to subhorizontal flexures, forming domed arch with diameter less than thecal max. just below radial summit; posterior oral larger, separating BC and DE orals.

REMARKS

L. pansus is variable in development of protrusions on orals and may develop a weak node distally on the radials. Without careful observation *L. pansus* could be considered a juvenile or variant of *L. protuberans*. However, the species differs from *L. protuberans* by the greater lateral expansion, lack of strongly protruded radials and

more rounded dome shape of the oral circlet. It is the smallest form in the Callytharra fauna.

Litocrinus protuberans sp. nov.
(Fig. 8)

ETYMOLOGY
Latin *protuberosus*, protuberant; for the radials.

MATERIAL
Holotype QMF21440 from QML759, paratypes QMF21441 from QML758, QMF21442, 21443 from QML759, QMF21444 from QML760, QMF21445 from QML757, and other material QMF21560 (8) from QML757, QMF21561 (3) from QML758, QMF21562 (15) from QML759, QMF21563 (19) from QML760, QMF21564 (3) from QML761, QMF21565 (5) from QML757-761.

DIAGNOSIS
Radials with evenly rounded large protuberances.

DESCRIPTION
Thecae small, largest specimen 1.1mm high, 0.9mm wide, turbinate to pyriform, walls expand rapidly from base of radials to large protuberances in distal part of radials, capped by oral circlet, strongly pentalobate in oral view, unornamented. Basals fused, bear circular stem facet proximally, gently outflaring distally, forming lower 1/3 of cup. RR 5, slightly longer than wide, expanding rapidly upward, longitudinally concave proximally to strongly convex distally, transversely gently convex proximally strongly convex distally; large smooth growth protuberance on distal part of radial. No anal notch on plates. OO 5, slightly longer than wide to subequal to wider than long, slightly irregular outer surface, vertical to slightly inflared proximally, subhorizontal to gently arched distally. Posterior oral largest, separating BC and DE orals, bearing small hydropore or madreporite. Oral circlet slightly inset on radial summits.

REMARKS
Growth sequence from 0.4-1.1mm present in the 67 specimens studied. Initially the theca is equidimensional and the radial protuberances are recognisable but not domineering as the cup wall flares moderately and evenly from the stem facet to the radial protuberances. As growth continues radials elongate and the protuberance expands to become the most noticeable morphologic feature of the theca. The base of the cup is relatively narrow and most of the wall flaring is with the radials.

No other species of *Litocrinus* has as strongly protruded distal parts of the radials as *L. protuberans*. There is a large node in the centre of each radial on the Late Permian *L. palermoensis* (Strimple & Sevastopulo, 1982) from Sicily that is a later evolved form.

Family CATILLOCRINIDAE Wachsmuth and Springer, 1886.

Notiocatillocrinus Willink, 1978

TYPE SPECIES
Notiocatillocrinus oakiensis Willink, 1978, from the Lower Permian of NSW; by original designation.

Notiocatillocrinus callytharraensis
Webster, 1987 (Fig. 14E)

Notiocatillocrinus callytharraensis Webster, 1987: 108, figs 7, 8.

MATERIAL
One weathered crown NMVP127202 from Fossil Hill, Bidgermia Station, GR351884 on Glenburgh 1:250,000 Geological Sheet SG 50. Collected by G.A. Thomas.

REMARKS
This is the largest specimen known. It is twice the length of the holotype and displays an excellent cross-section of the cup and tegmen.

Easily recognisable radials, showing the multiple arm facets, cups and the horseshoe-shaped tegmen plates of *N. callytharraensis* were found at every locality visited. Often they were embedded in the grainstones and not retrieveable without excessive labour. These plates make excellent index fossils in the Callytharra Formation throughout the Carnarvon Basin.

Superfamily BELEMNOCRINOIDEA Miller, 1883
Family SYNBATHOCRINIDAE Miller, 1889

Synbathocrinus Phillips, 1836

TYPE SPECIES
Synbathocrinus conicus Phillips, 1836 from the Lower Carboniferous of England; by monotypy.

Synbathocrinus constrictus (Wanner, 1916)
(Figs 9, 10A-H)

MATERIAL
Figured specimens QMF21460, 21461, 21463, 21465,

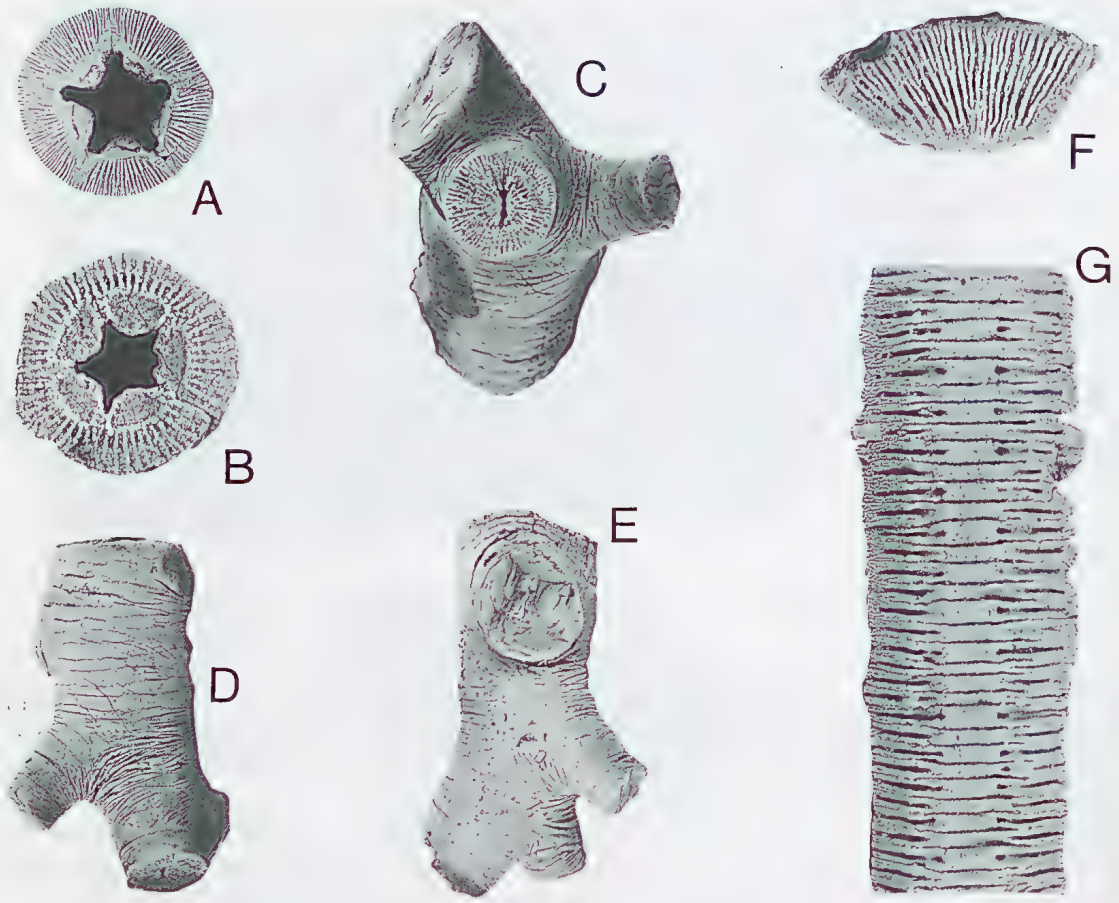


FIG. 12. Barycrinid? gen. indet. A, articular facet of pentameric columnal QMF21434, ×1.4. B, articular facet of pentameric pleuricolumnal QMF21435, ×1.7. C-E, root holdfast with branchlets or cirri, QMF21436, ×1.4. C, enlargement of articular facet of non-pentameric rootlet cirri. D,E, lateral views of holdfast in possible growth position. F,G, articular facet and inner lateral views of weathered pleuripentamere QMF21437, ×1.8.

21466, 21478, 21479 from QML759, QMF21462 from QML758, QMF21464, 21467 from QMl757 and other material QMF21571 (23) from QML757, QMF21572 (3) from QML758, QMF21573 (37) from QML759, QMF21574 (7) from QML760, QMF21575 (1) from QML761, and QMF21576 (6) from QML758-761.

REMARKS

Articulated thecae of juvenile and adult specimens of *Synbathocrinus constrictus* are moderately abundant throughout the interbedded arenaceous shales and limestones of the lower fossiliferous part of the Callytharra Formation at Callytharra Springs. Juvenile spec-imens are 0.4-2.5mm high and include growth stages from the armless embryonic through 5-armed forms.

Early growth stages are dominated by inflated orals and protuberant radials with a low narrow basal circlet. Radials and orals increase in length rapidly, are approximately equal in height and are the most obvious plates in the theca during early development. Radials show an early development of the medial longitudinal ridge, whereas orals are initially inflated then gradually develop a shallow central depression. The CD oral is largest, adjoining all other orals, separating the BC and DE orals, and bearing a small central protuberance, the hydropore or madreporite. At 1.3mm thecal height radials are approximately twice the height of the oral circlet and the first radial facet develops on the E radial. Growth continues in a linear increase greater than transverse until approximately 2.5mm height when lateral expansion is rapid. Arms develop in sequence in the C, B, D and A

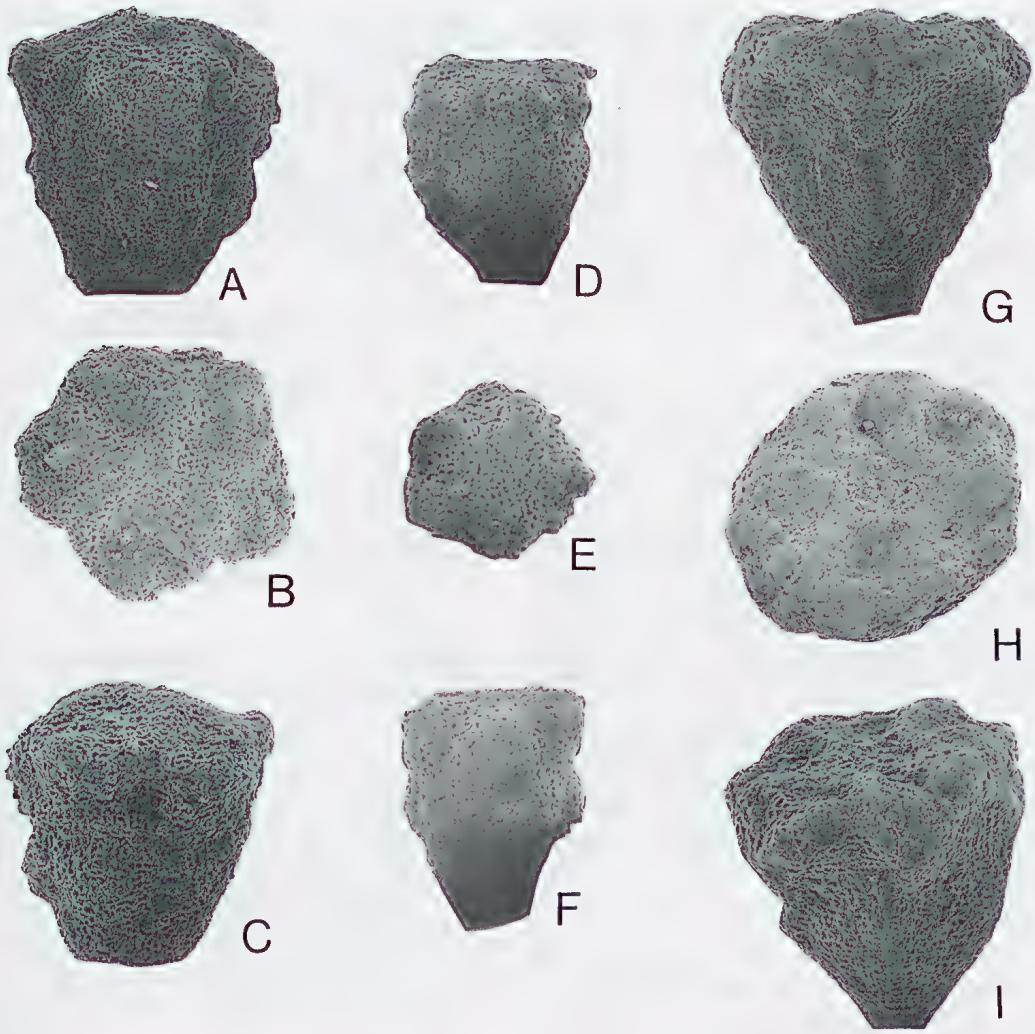


FIG. 13. *Lampadosocrinus variabilis* sp. nov. A-C, A ray, oral and C ray views of paratype QMF21451, ×40. D-F, A ray, oral and DE interray views of paratype QMF21452, ×40. G-I, E ray, oral and C ray views of holotype QMF21450, ×40.

rays. Only single specimens of most of the different arm stages are known. It is not known if the same sequential arm development is regularly followed. Orals are retained with the development of the fifth arm and the anal plate is not developed although a faint depression may occur in the radial circlet at the mutual shoulders of the C and D radials below the posterior oral. Macro specimens lack the oral circlet and were illustrated by Webster (1987).

Two abnormal specimens lack part or all of the fifth ray. One (Fig. 8G,H) has 4 radials and 4 orals. Except by careful examination it appears to be a normal 5 rayed theca. The other (Fig. 7F,G) has a partial fusing of the A and B radials and orals are distorted.

Small brachials up to 2.5mm long in the disarticulated washings are judged to be the beginning growth stages of arms of *S. constrictus* on the basis of the articular facet and the medial longitudinal ridge. Two of these brachials are illustrated to show the variation in longitudinal curvature, shape, ambulacral groove and distal tips.

These thecae are assigned to *S. constrictus* because they show the prominent radial ridge. Webster (1987) noted the gradation between *S. constrictus* and *S. campanulatus* so some of these

may be immature specimens of *S. campanulatus* but that form is not recognised until its adult stage.

Family UNCERTAIN

Microcrinoid holdfasts gen. et sp. indet.
(Fig. 10I-M)

MATERIAL
QMF21475-21477 from QML759 and QMF21577 from QML757-761 west of Callytharra Springs.

DESCRIPTION
Base hexagonal, rectangular or irregularly polygonal; sides scalloped to irregular; thickened centrally or towards one end extending as base of round columnal. Base concave.

REMARKS
Holdfasts 1.0-2.0mm long, 0.5-1.5mm wide and 0.6-1.0mm high. They range from Early Carboniferous in the United States (Webster, unpubl. data) to the Permian. They are illustrated for comparison in future studies and to demonstrate the scope of the Callytharra echinoderm fauna.

Order CLADIDA Moore &Laudon, 1943
Suborder CYATHOCRININA Bather, 1899
Superfamily CYATHOCRINITOIDEA Bassler, 1938
Family CYATHOCRINITIDAE Bassler, 1938

Occiducrinus Webster, 1990

TYPE SPECIES
Occiducrinus australis Webster, 1990 from the Artinskian Wandagee Formation, Minilya River, W.A.; by original designation.

Occiducrinus australis Webster, 1990
(Fig. 11B-D)

Occiducrinus australis Webster, 1990:60, pl. 2, figs 1-3.

MATERIAL
QMF21427 from the third thick sandstone bed above the base of the Artinskian Wandagee Formation, east limb of syncline, approximately 150m north of the Minilya River, Coolkilya Pool area, Wandagee Station, Western Australia.

REMARKS
This cup was weathering out as associated disarticulated plates on a bedding surface which also yielded *Eoindocrinus praecontignatus* and *Calceolispongia abundans*. The reconstructed cup lacked the anal, the D radial and the orals; it is nearly identical in size with the holotype.

The proximal columnal showing the articulum provides information not preserved on the holotype. Crenularium narrow; culmina short, widely spaced; crenellae wide, flat base, bearing rudimentary short ridges and V-shaped protrusions along irregularly walled outer side. Areola three times width of crenularium. Disarticulated columnals should be easily recognised.

Family BARYCRINIDAE Jaekel, 1918

Barycrinid? indet.
(Figs 12, 22D)

MATERIAL
Figured specimens QMF21434, 21436 from QML760, QMF21435 from QML761, QMF21437 from QML757. Other material QMF21586 from QML757 and QMF21587 from QML760.

DESCRIPTION
Columnals circular, pentameres; latus gently convex; heteromorphic type I pattern; symplexy articulation. Crenularium 1/3 radius on small columnals, may be more on large columnals, projects into areola at pentamere boundaries on some specimens. Culmina irregular, medium width, wider distally, may divide isotomously once; new culmina may be inserted distally. Areola 1/3 radius on small columnals, may be less on large columnals, sloping inward, smooth. Axial canal strongly pentastellate; claustrum narrow, thin, wedge-shaped, forms base of areola. Cirri circular in section, short, tapering rapidly distally, not divided into pentameres; latus straight; articulum same as pentamere articulum; axial canal narrow, slightly dumb bell-shaped transversely.

REMARKS
All pluripentameres (up to 4.95cm length) and pluricolumnals of articulated pentameres were recovered as loose specimens. Weathering destroyed many morphologic features but especially the claustrum on pluripentameres. Differentiated weathering resulted in irregular wavy thickness on external surfaces of some columnals (Fig. 22D). Most of the larger specimens are part of the holdfast or distal parts of the stem. The robust size suggests they supported a sizeable crown. It is unknown if the pentameres extended to the cup.

Pentameric columnals are present on several inadunates and camerates of Ordovician through Devonian age (Moore & Jeffords, 1968). Middle

Mississippian *Barycrinus* from Iowa are the previously recognized youngest pentameric stems (Moore et al. in Moore & Teichert, 1978). We refer these specimens questionably to the Barycrinidae and illustrate them because they are easily recognizable, have potential as Permian index fossils in the Carnarvon Basin and extend the geographic and stratigraphic range of pentameric columnals.

Superfamily CODIACRINOIDEA Bather, 1890
Family STREBLOCRINIDAE Lane, 1967

Lampadosocrinus Strimple & Koenig, 1956

TYPE SPECIES

Dichostreblocrinus minutus Peck, 1936 from the Lower Carboniferous St. Joe Formation, USA.

Lampadosocrinus variabilis sp. nov.
(Fig. 13)

ETYMOLOGY

Latin *variabilis* variable; refers to the variation in shape of the oral circlet, and number of infrabasal plates.

MATERIAL

Holotype QMF21450 from QML757-761 undifferentiated, paratypes QMF21451 from QML759, QMF21452 from QML757-761, QMF21453 from QML757, QMF21454 from QML758, QMF21455-21459 from QML759 and other material QMF21566 (5) from QML757, QMF21567 (2) from QML758, QMF21568 (24) from QML759, QMF21569 (2) from QML760, QMF21570 (5) from QML757-761.

DIAGNOSIS

Oral plates of variable shape; theca inflated; basals tumid.

DESCRIPTION

Theca small, conical, subcylindrical to widely inflated, widest at or slightly below oral summit, height/width ratio 1.0-1.4, surface ornament of minute pits.

IBB 1-5, most commonly fused; circlet low, narrowly to moderately outflared, pentalobate to circular transversely, forming lower 1/2 of cup, 1/4 of theca, bearing small impressed circular stem facet. BB 5, with variable length to width ratio, wider than long, subequal to longer than wide, convex transversely and longitudinally, tumidity gentle to moderately strong, rarely projecting into a short spine. OO 5, roundly to sharply protruded at or barely below thecal summit, oral surface inflated to depressed centrally, sutures flush to elevated along mutual narrow ridges. CD oral largest, protuberance more rounded than others, separates BC and DE orals. Oral circlet forming 2/5 thecal height, with slightly concave summit, horizontal or slightly inflated, sutures align with basal suture, rotated slightly or in normal alternate position. BC and DE oral protuberances commonly slightly down and outflared, EA and AE oral protuberances normally subhorizontal. No anal plates, BC basal left shoulder summit slightly below CD right shoulder summit; all other basal summits align.

REMARKS

Variation among the 47 specimens studied reflects growth changes and intraspecific variation. Two changes with growth are height/width ratios of the oral plates. In general elongation of the theca progresses from subequal height and width in immature forms to height greater than width in adult forms. Ratios in a growth series of 4 specimens calculated as 1.0, 1.4, 1.06, 1.11, smallest to largest. Oral plates of immature specimens are commonly roundly protuberant, rarely pointedly protuberant, and lack the rimmed depression on the summit typical of larger specimens. In immature forms the five protuberances project above the summit slightly, forming a slightly depressed summit. With growth the rimmed depression develops on each of the orals while the central oral summit is normally gently inflated forming the highest point on the theca. On the largest individuals the summit is commonly horizontal.

Intraspecific variation is noted in the following features. Most specimens are inflated moderately with only a few specimens having mildly inflated subcylindrical walls above the infrabasals. The angle of outflaring to the protuberances on the orals is variable. Tumidity of the basals ranges from slight to moderate and rounded to elongate in outline; rarely the tumidity is a short sharpened projection or blunt spine. Sharpness of the oral tumidity varies from rounded to angular and directed subhorizontal to gently upflared.

Suborder POTERIOCRININA Jaekel, 1918
Superfamily SCYTALOCRINOIDEA Moore & Laudon, 1943
Family APHELECRINIDAE Strimple, 1967

Cosmetocrinus Kirk, 1941

TYPE SPECIES

C. gracilis Kirk, 1941 from the Mississippian of Indiana; by original designation.

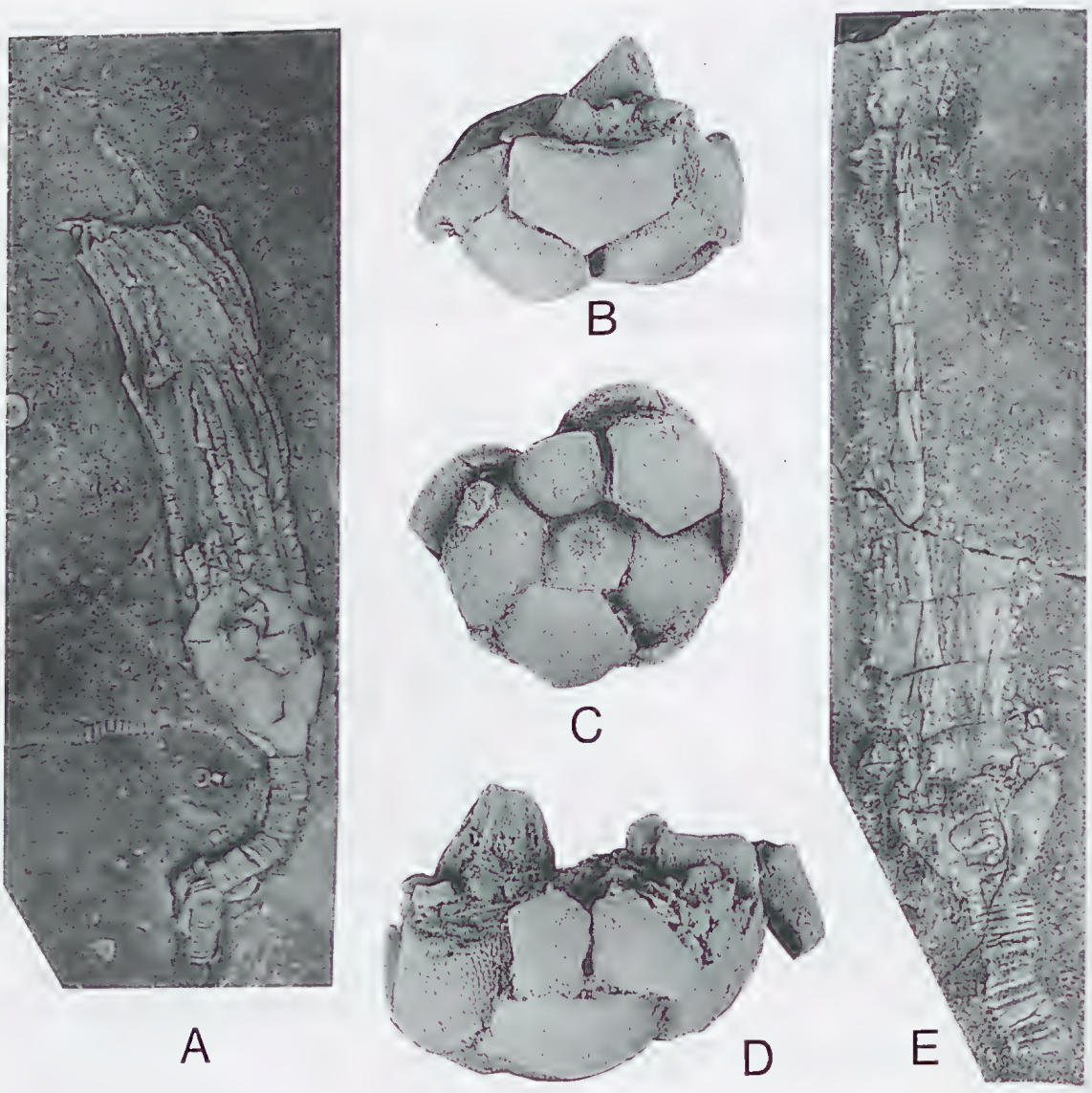


FIG. 14. A, *Cosmetocrinus? middalyaensis* sp. nov., posterior view of holotype UWAF113385, ×0.7. B-D, *Trautscholdicrinus* sp. A ray, basal and posterior views of WAM67.529, ×3. E, *Notiocatillocrinus callytharraensis* Webster, 1987, weathered crown showing cross-section of cup and tegmen, NMVP127202, ×1.1.

Cosmetocrinus(?) middalyaensis sp. nov.

(Fig. 14A)

ETYMOLOGY

For Middalya Station.

MATERIAL

Holotype UWAF113385 from QML770. Collected by John Williamson.

DIAGNOSIS

Right tube plate not in contact with the radianal.

DESCRIPTION

Crown tall (119mm), cylindrical (23.3mm wide maximum), plates smooth. Dorsal cup conical, flattened, approximately equidimensional, 22.6mm long, 22mm wide at summit, base flat, walls slightly convex proximally, slightly outflared distally. IBB 5?, large, 7mm long, 7mm wide, steeply upflared. BB 5, large, CD longer

(13.1mm) than wide (7.5mm), mildly convex transversely and longitudinally. RR 5, large, 7.8mm long, 7.8mm wide, mildly convex transversely and longitudinally. Radial facets plenary, sloping outward, with well developed transverse ridge and outer ligament pit; slight gape between radials and primibrachials. Anals 3, radianal narrow, in oblique position, adjoins C radial, BC and CD basal and anal X; anal X largest, 6.3mm long, 4.8mm wide, adjoining right tube plate, C radial, radianal, CD basal, D radial, and 2 tube plates, distal tip above radial summit; right tube plate nearly excluded from cup, only proximal tip below radial summit, not in contact with radianal. IBrr one per ray; in C and D rays, longer (8mm) than wide (6.6mm), constricted distally, strongly convex transversely, axillary. IIBrr, IIIBrr and IVBrr cuneate, strongly convex transversely. All branching isotomous. Second branching on IIBr8-10, one additional branching in some rays. Total number of arms exceeds 20 per ray if branching uniform in all rays. Pinnules small, slender. Anal sac tall, slender, mostly covered. Stem round transversely, heteromorphic, thin columnals, type II patterns for proximal 40mm, homeomorphic thick columnals distally; total of 130mm of stem preserved. Columnal latus convex, symplexy articulation. Non-cirriferous.

REMARKS

Radials of this species were described as inadunate radial #7 (Webster, 1987) based on loose radials found at Callytharra Springs approximately 250km to the south. *C.? middalyaensis* is widespread in the Carnarvon Basin and the radials are sufficiently distinct to be identified when disarticulated.

The crown is crushed in situ as it retains the arms and considerable length of the stem. Erosion has removed, but left the impression of, the distal 30mm of the arms. Generic assignment remains tentative because the A ray is not exposed to determine if branching occurs on the first primibrachial or a higher primibrachial as in *Paracosmetocrinus*. Some species of *Paracosmetocrinus* have a strongly cirriferous proximal stem, which is not present in *C.*(?) *middalyaensis*. The number of infrabasals is also uncertain as only one complete and one partial infrabasal are exposed. Their size and position suggests there are only three infrabasals on this form.

Crinoids associated on the slab are a weathered crown of *Texacrinus granulosus* sp. nov., disarticulated columnals of a camptocrinid and at least five unidentified crinoids. In addition several specimens of the spiriferid brachiopod *Fusispirifer carnarvonensis* Archbold & Thomas, 1987 and fenestrate bryozoans are present.

Elevation of the right tube plate until it is nearly eliminated from the cup is an advanced condition, suggesting a younger age than the Early Carboniferous age of previously described species (Moore & Teichert, 1978). Aphele-crinids were previously known only from the Lower Carboniferous of North America and Europe (Moore &Teichert, 1978).

Superfamily AGASSIZOCRINOIDEA Miller, 1889

Family AMPELOCRINIDAE Kirk, 1942

Spheniscocrinus Wanner, 1937

TYPE SPECIES

Spheniscocrinus spinosus Wanner, 1937 from the Permian of Timor; by original designation.

Spheniscocrinus australis sp. nov.
(Fig. 11A)

ETYMOLOGY

Latin *australis*, southern.

MATERIAL

Holotype crown CPC30682 from the Artinskian upper Bulgadoo Shale or lower Cundlego Formation, 7.5km on bearing 287° from Wandagee Homestead, Minilya 4 mile map sheet, Carnarvon Basin.

DIAGNOSIS

Ornament shagreen with small pits; sutures flush; spines on brachials without nodes.

DESCRIPTION

Crown small, low, outspreading laterally, estimated 60mm diameter; ornament of small depressions on very fine shagreen surface. Cup low bowl to discoid-shaped, 5.7mm wide, 2.2mm high (estimated), shallow apical pits. IBB 5, impressions small, probably subhorizontal. BB 5, small, convex transversely and longitudinally, unequal size; EA estimated 1.3mm long, 1.2mm wide; CD 2.1mm long (estimated), 2mm wide. RR 5, wider (1.8mm) than long (1.3mm), gently convex longitudinally, strongly convex transversely, thick, spreading laterally proximally resulting in wide gap between radials at summit. Radial facet plenary, slope steeply outward, thick, small gaps. Anals 3, in intermediate position. Radianal in oblique position intermediate in size. Anal X largest, strongly convex transversely, adjoins posterior basal. Right tube plate smallest, not in contact with

FIG. 15. *Minilyacrinus williamburyensis* sp. nov., posterior and B ray views of weathered holotype crown, WAM91.697, ×1. C, fragmentary set of arms, UWAF113504, ×1.5.

radianal, proximal end barely below radial summit, admedial to anal X, barely visible in lateral view. IBrr 2 per ray, rectilinear, wider than long, thick, straight longitudinally, strongly convex transversely; axillary $IBrr_2$ constricted slightly proximally. IIBrr and IIIBrr cuneate, wider than long, thick, strongly convex transversely. All branches isotomous on IBr_2 and $IIBr_8$, minimum 4 arms per ray. Pinnules moderately large but not ramules, one per brachial on alternate sides of arm. Stem and tegmen not known.

REMARKS

This crown is inverted with the arms splayed outward on the substrate. The stem, infrabasal circlet and parts of most basals are not preserved but impressions of the inner side of the infrabasals and basals are moderately clear. The anal series extending into the base of the anal tube or sac is large, nearly the size of the base of the arms.

Spheniscocrinus was defined by Wanner, 1937, as having only one anal in the cup, however, the holotype and only specimen appears to be slightly distorted in the base of the C ray and adjacent anal series. It may have an intermediate arrangement of the anals as described above.

This is only the second member of the genus and is distinguished from the type species by the fine shagreen ornament, flush sutures and lack of nodes or spines on the brachials. Generic distribution is extended to Western Australia strengthening the link between Timorese and Western Australian Permian faunas.

SuperfamilyDECADOCRINOIDEABather,1890Family DECADOCRINIDAE Bather, 1890

Trautscholdicrinus Yakovlev & Ivanov in Yakovlev, 1939

TYPE SPECIES

Trautscholdicrinus miloradowitschi Yakovlev & Ivanov in Yakovlev, 1939, Upper Carboniferous Moscow Basin; by original designation.

Trautscholdicrinus sp.
(Fig. 14B-D)

MATERIAL

Partial crown WAM67.529, from the Artinskian Fossil Cliffs Formation, north branch Irwin River, Perth Basin. Found by Mrs J. White.

DESCRIPTION

Cup medium bowl-shaped, shallow basal invagination, walls subvertical, fine granular ornament. IBB 5, small, equidimensional (2.0mm)

kite-shaped, slightly upflared, not visible in lateral view. BB 5, hexagonal, wider (5.8mm) than long (5.0mm), moderately convex transversely, strongly convex longitudinally, proximally form base of cup, distally subvertical forming nearly half cup height, slightly tumid. RR 5, wider (5.7mm) than long (3.4mm) slightly convex longitudinally, moderately convex transversely. Radial facet plenary, sloping gently outward, bearing transverse ridge, outer ligament pit and furrow, and wide shallow muscle areas adorally. Anals 3, in intermediate position. Radianal largest, pentagonal, adjoins C radial, BC and CD basals, anal X and right tube plates. Anal X pentagonal, truncated CD basal, adjoining one tube plate distally. Right tube plate not preserved, proximal end barely below radial summit. A ray IBr1 axillary, strongly convex transversely. Distal brachials slightly cuneate, strongly convex transversely, bearing one pinnule each distally. Stem impression round.

REMARKS

The cup is crushed from compaction but plates are well preserved. The infrabasal circlet is not visible in lateral view and sutures appear slightly impressed because the tumidity of the basals projects above them. This is the second crinoid reported from the Fossil Cliff Formation after *C. digitata* (Teichert, 1949). The specimen is of insufficient quality to serve as a type. Radials like these occur in the disarticulated ossicles at Callytharra Springs.

Superfamily CROMYOCRINOIDEA Bather, 1890

Family CROMYOCRINIDAE Bather, 1890

Minilyacrinus gen. nov.

TYPE SPECIES

Minilyacrinus williamburyensis sp. nov.

ETYMOLOGY

For the Minilya River.

DIAGNOSIS

Cup bowl-shaped, with single anal; arms uniserial, cuneate, numbering 20.

Minilyacrinus williamburyensis sp. nov.

(Fig. 15)

ETYMOLOGY

For Williambury Station.

MATERIAL

Holotype WAM91.697 from an undesignated locality on Williambury Station. The specimen was enclosed in a quartz and mica bearing grainstone of the Callytharra Formation. It probably came from the vicinity of Donnelly's Well or other exposures of the Callytharra Formation in the eastern line of the Gooch Range in the southwestern part of Williambury Station. One partial set of arms (UWA) from the eastern line of the Gooch Range along the Minilya-Williambury Station road.

DESCRIPTION

Crown moderately large, 42.8mm long incomplete, average 13.1mm wide, cylindrical. Anal sac small cylindrical, formed of eight rows of plates. Cup moderately large, 13.9mm high, 23.1mm wide at summit, bowl-shaped; walls gently outflared distally; moderately deep basal invagination (7.1mm diameter); unornamented; sutures flush. IBB small, covered by proximal columnals, confined to basal invagination, probably downflaring. BB 5, large, slightly wider (8.8mm) than long (7.8mm), strongly convex longitudinally, moderately convex transversely, proximal ends within basal invagination, forming basal plane of cup; CD basal symmetrical, truncated distally for adjoined radianal. RR 5, large, wider (14.7mm) than long (9.7mm), moderately convex transversely, mildly convex longitudinally. Radianal longer (8.6mm) than wide (6.5mm), slightly over half above radial summit, adjoined distally by one tube plate. Radial facets plenary, sloping gently outward, moderate gape between radials and primibrachials. IBrr one per ray, wider (14.5mm) than long (8.1mm), moderately convex transversely, mildly convex longitudinally, axillary. IIBrr 2 per ray, wider (8.4mm) than long (4.1mm), strongly convex tranversely. IIIBrr wider than long, slightly cuneate, strongly convex transversely, thick, pinnulate. Ambulacral groove narrow, deep. Branching isotomous, 20 arms. Stem heteromorphic; columnals circular transversely, lumen pentagonal, symplexy articulation.

REMARKS

The partial crown has been deeply weathered on exposed surfaces, the distal part of the arms and anal sac are lost, slight crushing occurred oblique to the A-CD symmetry plane, and arms adjacent to the anal series have been disarticulated in part. Weathering along the flush sutures of the cup plates and into cleavage planes in the calcite plates appear as deep impressions. A small portion of the B and C rays, including radials and adjacent basals were enclosed in matrix and unweathered.

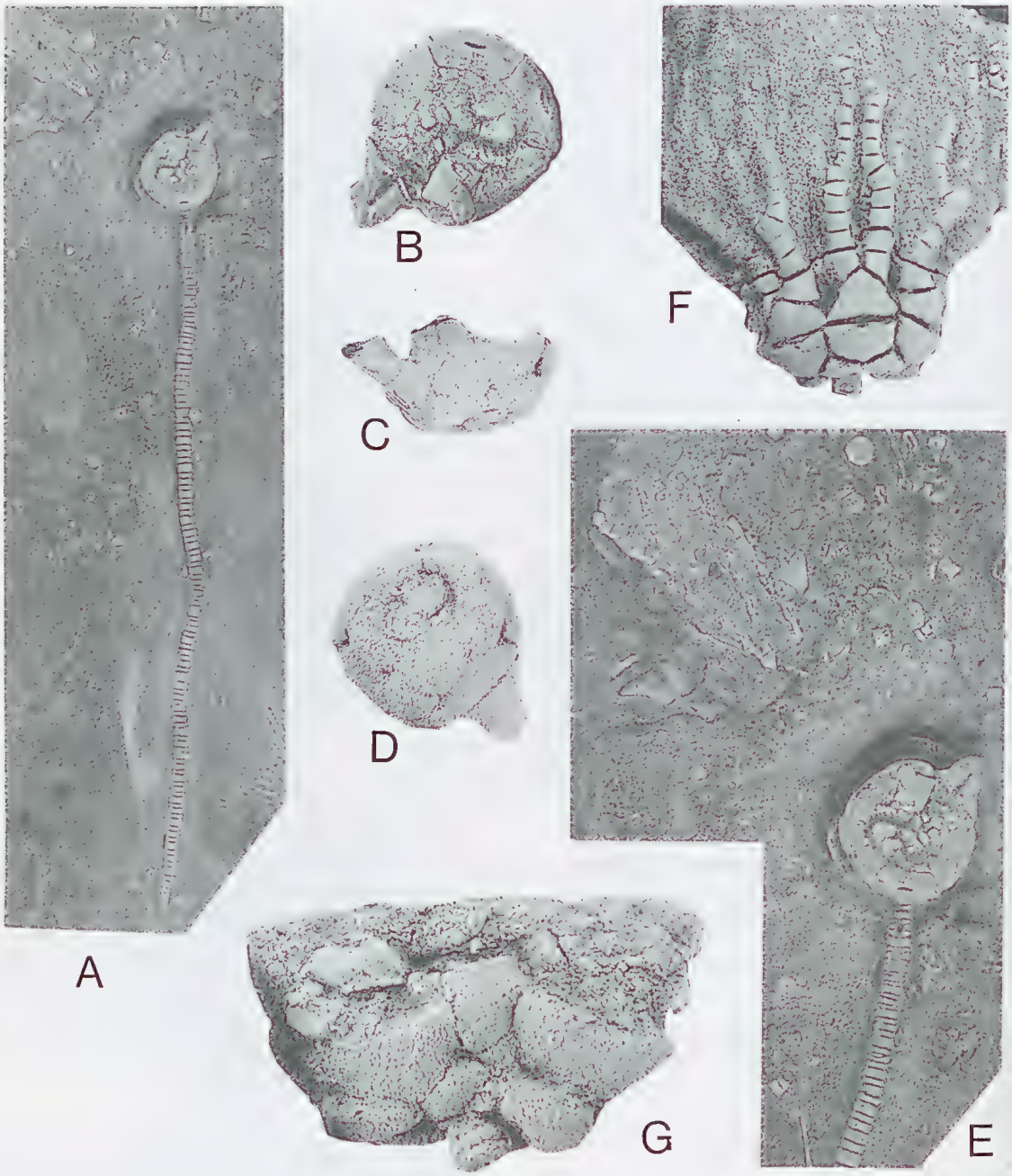


FIG. 16. *Texacrinus goochensis* sp. nov. A-E, paratype UWAF115099. A, weathered crown showing attached stem, ×1. B-D, oral, posterior and basal views of dorsal cup with attached primibrachial, ×3. E, enlargement of part of A showing parts of arms to upper left and directly above cup and change in heteromorphic patterns, proximally type II to distally Type I, ×2. F,G, lateral and posterior views of holotype crown UWAF 113387, F ×2; G ×3.5.

Removal of the matrix exposed the lack of ornamentation and flush sutures.

The partial set of arms show the tapering distal arm tips of slight cuneate shapes typical of the cromyocrinids. Thickness of the plates, narrow ambulacral grooves, strong external convexity and slight cuneate shape of the brachials is similar to that of uniserial brachials in the Cromyocrinidae. However, cup plates lack the impressed sutures typical of smooth plated cromyocrinids with uniserial arms (Webster, 1981).

The single anal and multiple arms reflect an advanced evolutionary condition. This is the first cromyocrinid bearing uniserial arms to be recognised with more than 10 arms, whereas many biserial armed cromyocriniods have 12 to 19 arms (Webster, 1981).

Evolution of *Minilyacrinus* is uncertain, perhaps through *Cromyocrinus*, *Goleocrinus* or *Mooreocrinus* by increase in arm number, reduction of the number of anals in the cup and increase in depth of the basal invagination. Evolution from *Moapacrinus* would only require increase in arm number.

The Cromyocrinidae is an Early Carboniferous to Early Permian family with greatest generic and specific diversity in the Late Carboniferous (Webster, 1981). They have been reported from North and South America and Eurasia. Webster (1981) considered all Permian forms from Timor, Russia and India previously referred to the cromyocrinids to belong to an unnamed genus or genera of non-cromyocrinid stock. Only two cromyocrinids, *Moapacrinus* and an unnamed genus, are of Permian age. Both are from the southwestern United States, have only one anal, and the 10 arms are uniserial on *Moapacrinus* but unknown on the unnamed genus (Webster, 1981).

Minilyacrinus is the first cromyocrinid from Western Australia. The partial set of 10 arms identified as Poteriocrinidae gen. ind. et. spec. nov. ind. (Wanner, 1949, pl. 3, fig. 31) from Timor probably belongs to a cromyocrinid.

Superfamily ERISOCRINOIDEA Wachsmuth & Springer, 1886

Family GRAPHIOCRINIDAE Wachsmuth & Springer, 1886

Tapinocrinus Webster, 1987

TYPE SPECIES

Tapinocrinus macurdai Webster, 1987 from the Artinskian Callytharra Formation, W.A.; by original designation.

Tapinocrinus spinosus Webster, 1990
(Fig. 11E)

MATERIAL

WAM91.696 from the Wandagee Formation, north side Minilya River, Coolkilya Pool area, Wandagee Station, Western Australia; collected by H. Coley.

REMARKS

A second specimen of *Tapinocrinus spinosus*, 42.5mm long, 20.1mm wide, shows the delicate shape and pointed apex of the fully enclosed crown. A very fine shagreen ornamentation is preserved along the arm sutures on brachials of the D ray. This is not preserved on the specimen reported by Webster (1990).

SuperfamilyTEXACRINOIDEAStrimple, 1961
Family TEXACRINIDAE Strimple, 1961

Texacrinus Moore & Plummer, 1940

TYPE SPECIES

Texacrinus gracilis Moore & Plummer, 1940 from the Middle Pennsylvanian, Millsap Lake Formation, Texas; by original designation.

Texacrinus goochensis sp. nov.
(Fig. 16)

ETYMOLOGY

For the Gooch Range.

MATERIAL

Holotype UWAF113387, a crown collected by Chris Hearne; paratype UWA115099 collected by John Williamson from QML770.

DIAGNOSIS

Ornament granulose.

DESCRIPTION

Crown small, weakly outflared, anal sac unknown, granulose ornament on cup plates and proximal brachials. Dorsal cup small, low bowl-shape, nearly three times wider than high, widest at radial summit, moderately deep basal invagination, sutures flush to gently impressed, moderate pits at apices of basals and radials. IBB small, confined to basal invagination, covered by proximal columnals, probably downflared. BB 5, wider than long, tumid, forming walls of invagination proximally, basal plane of cup medially, lower part of gently outflaring walls of cup distally, distal tip incurved; posterior basal may be

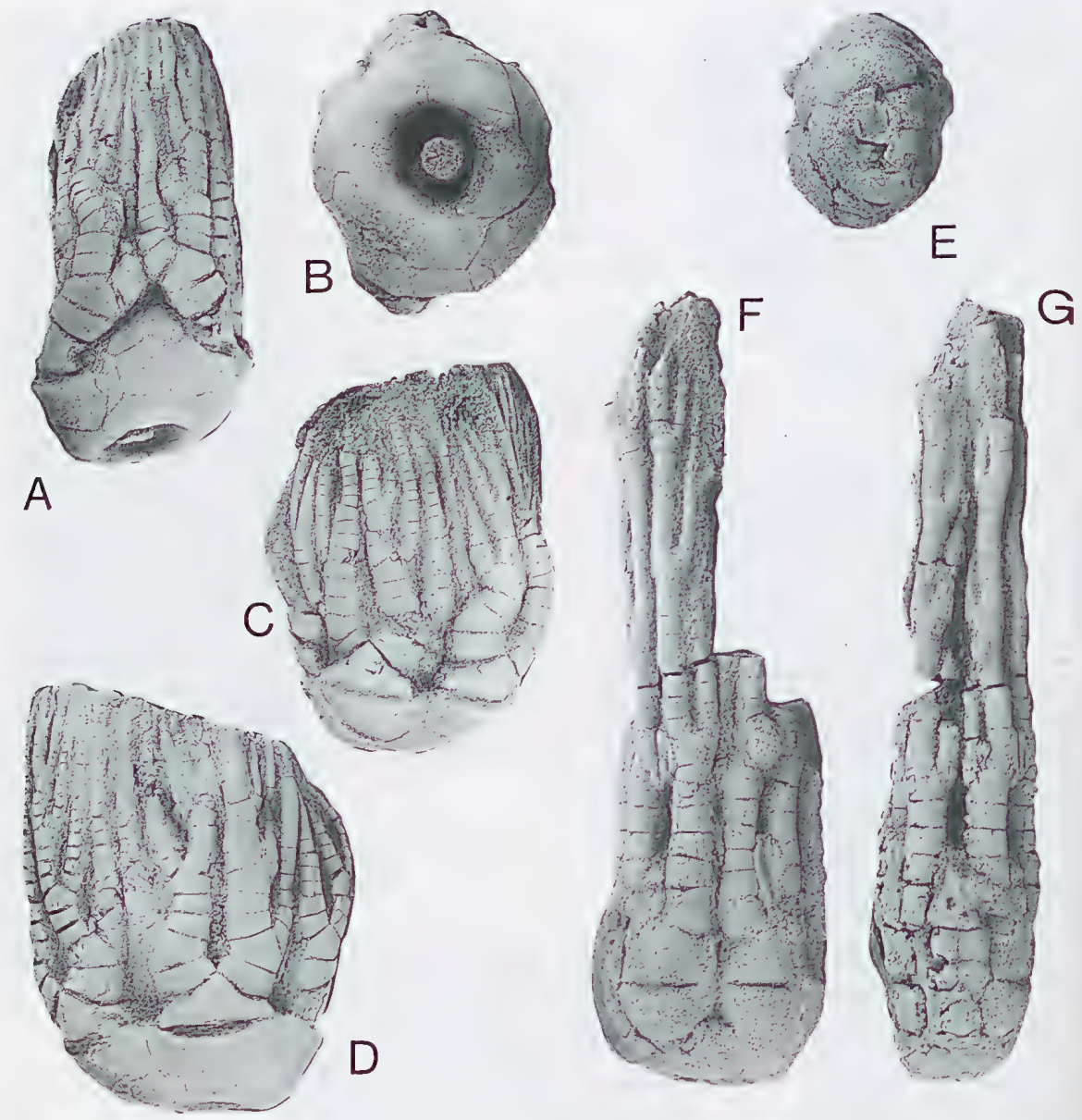


FIG. 17. A-D, *Texacrinus gascoynensis* sp. nov., posterior, basal, BC interray and B ray views of holotype WAM91.698, ×1. E-G, *Texacrinus hardmanensis* sp. nov., basal, BC interray and posterior views of holotype CPC30683, ×1.5.

truncated distally for anal X. RR 5, approximately twice as wide as long, mildly convex transversely and longitudinally, tumid, outflared. Radial facets plenary, sloping outward gently, with well developed transverse ridge, outer ligament pit and muscle fields. Anals 3 in primitive or modified primitive arrangement, variable in relative sizes. Radianal pentagonal or hexagonal, may or may not adjoin D radial, longer than wide. Anal X longer than wide, 0.5-0.67 below radial summit, adjoining one tube plate distally. Right tube plate small, proximal 1/3 below radial summit, adjoining one tube plate distally. IBrr one per ray, wider than long, constricted distally, strongly convex transversely, unequal in length (A ray longest), axillary. IIBrr to VIBrr slightly cuneate, equidimensional to wider than long, branching on 4th or 5th brachial in each series. First branch

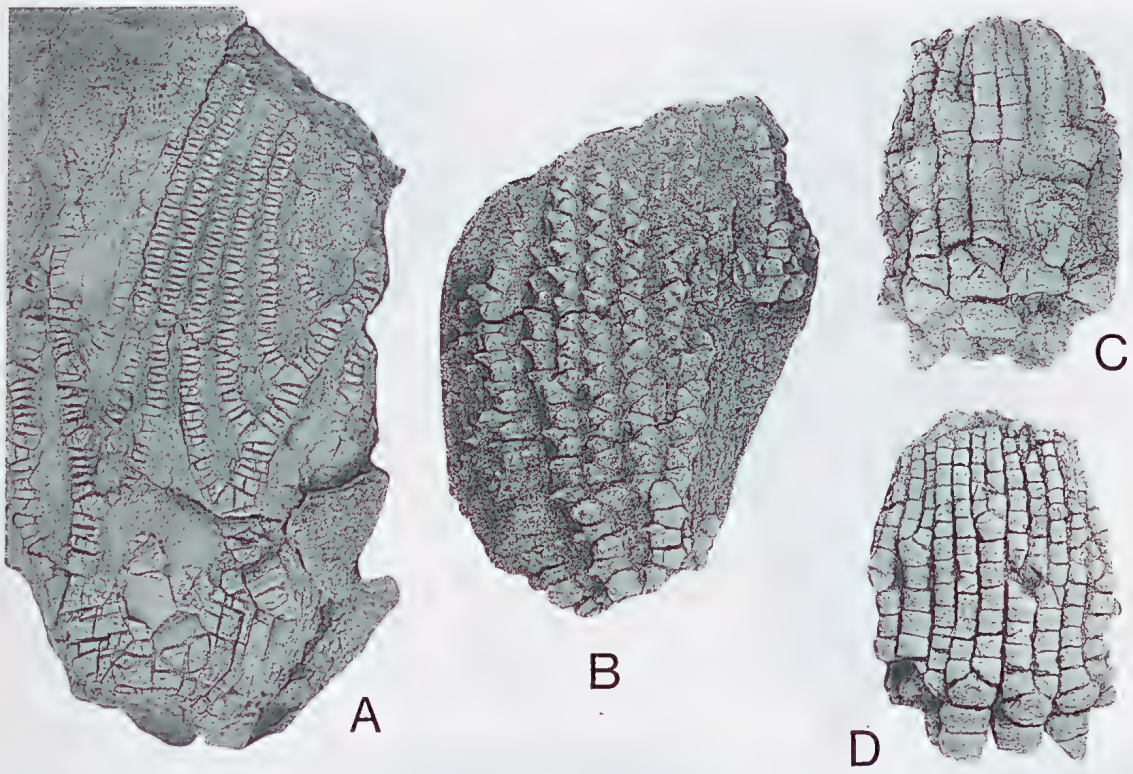


FIG. 18. A, *Galateacriuus australis* sp. nov., anal view of holotype UWAF113388, ×1. B, Family and genus indet., lateral view of set of arms QMF21469, ×1.6. C,D, Timorechinid indet., lateral views of set of arms, QMF21468, ×1.6.

isotomous, thereafter heterotomous bi-exotomous, 30 to 50 arms. Stem round, columnals thin heteromorphic type II pattern proximally, thicker heteromorphic type I pattern distally, latus convex, non-cirriferous, lumen pentagonal.

MEASUREMENTS (mm)

	Holotype UWA113387	Paratype UWA113385
Crown length	29.9 (incomplete)	35.0
Crown width	32.8 (at IIIBr)	-
Cup height	4.3	3.6
Cup width	11.8 (average)	9.9
Basal length	2.6	2.6
Basal width	3.6	3.6
Radial length	2.9	3.3
Radial width	6.0	5.9
IBr1 length	4.4	3.3
IBr1 width	6.0	4.5
Diam.proximal columnal	2.2	2.3

REMARKS

The holotype is a crushed crown lacking the distal parts of the arms with the anals in primitive arrangement; the radianal is in oblique position not in contact with the D radial. Weathering of the paratype has removed all except one primibrachial and distal parts of the arms of two rays. The paratype has anals in a slightly advanced arrangement; the radianal adjoins the D radial separating anal X from the CD basal. The slightly advanced arrangement of the anals has been reported in all species previously assigned to the genus suggesting that it has been a fairly stable genetic character since the middle Pennsylvanian.

Texacrinus has been reported from middle Pennsylvanian to Early Permian strata of the United States (Webster, 1973). Variables within the family are degree of suture impression (slight to moderate), depth of basal invagination (slight to deep), development of apical pits (not present to moderately deep), cup shape (slightly globose to weakly outflared low to medium bowl), and brachial form (nearly flat to strongly convex transversely; rectilinear to slightly cuneate, very

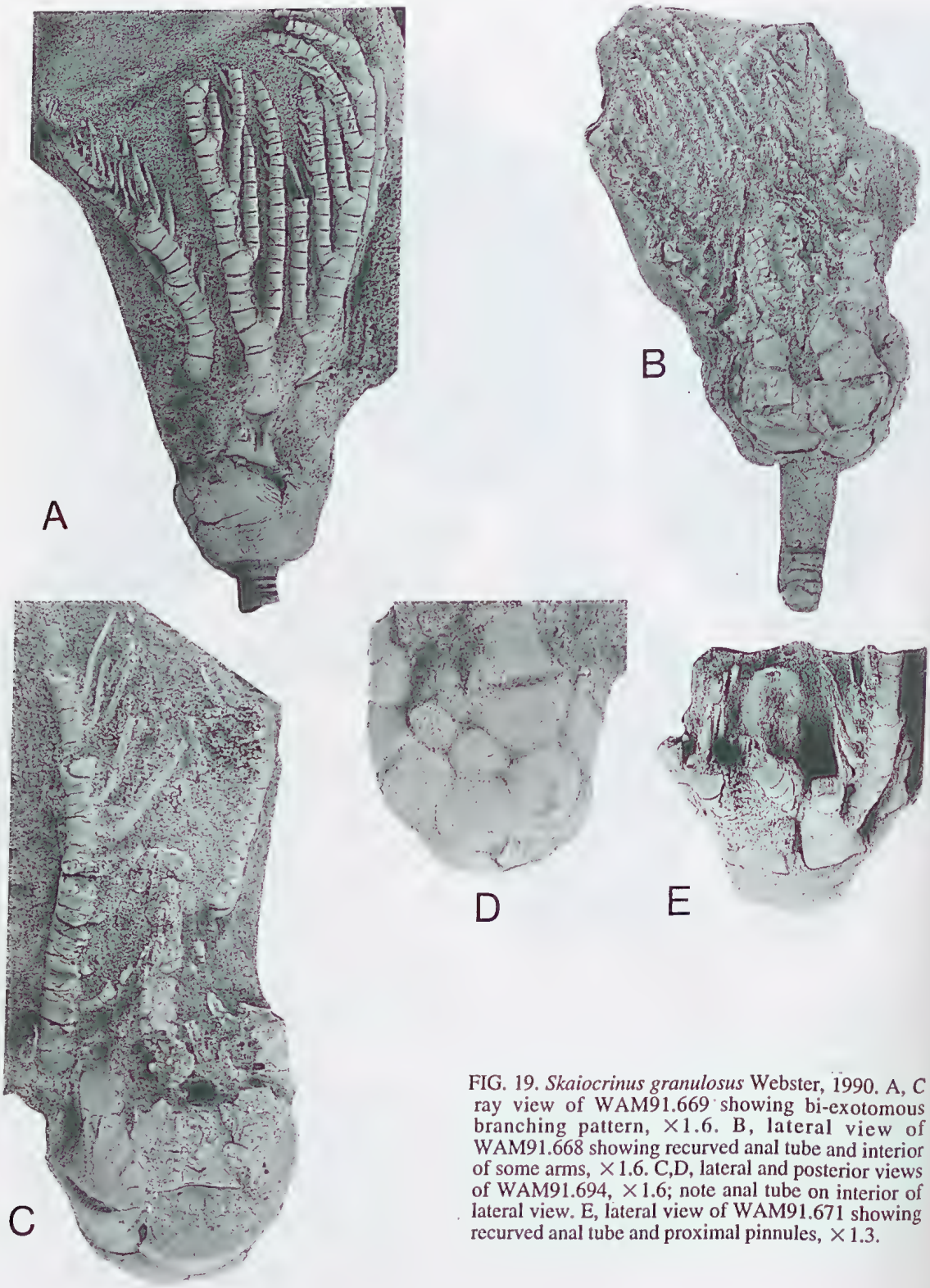


FIG. 19. *Skaiocrinus granulosus* Webster, 1990. A, C ray view of WAM91.669 showing bi-exotomous branching pattern, ×1.6. B, lateral view of WAM91.668 showing recurved anal tube and interior of some arms, ×1.6. C,D, lateral and posterior views of WAM91.694, ×1.6; note anal tube on interior of lateral view. E, lateral view of WAM91.671 showing recurved anal tube and proximal pinnules, ×1.3.

short to short). Where known, the arms branch bi-exotomous after an initial isotomous division. We consider *T. interruptus*, *T. irradiatus* and *T. compactus* named by Strimple (1952) and all from the Francis Shale of Oklahoma to be one species showing slight to moderate variation in many of the cup features listed above. We select *T. irradiatus* to be the senior synonym because the holotype is a more complete individual and intermediate in the range of variation.

Texacrinus goochensis extends the geographic range of the genus to Western Australia and is the first species named with granulose ornament.

Texacrinus hardmanensis sp. nov.
(Fig. 17E-G)

ETYMOLOGY
For Mount Hardman.

MATERIAL
Holotype CPC30683, a partial crown, from the Tatarian Cherrabun Member, Hardman Formation, at Mt. Hardman, Canning Basin. BMR localities KLB 11.

DIAGNOSIS
Anals in intermediate position with proximal tips of anal X and radianal below summit; arms elongate.

DESCRIPTION
Crown elongate (68.5mm, slightly incomplete), cylindrical, widest at radial summit, no arm girdle, fine vermiform to granular ornamentation on all plates, crushed slightly normal to plane of symmetry. Cup bowl-shaped, wider (16.3mm average) than high (9.7mm), base invaginated, sutures shallowly impressed, shallow apical pits. IBB 5?, covered, small, probably downflared, not visible in lateral view. BB 5, wider than long (C basal 6.4mm wide, 5.9mm long), gently convex transversely, moderately convex longitudinally, forming base of cup proximally; CD basal truncated distally for radianal. RR 5, wider (8.9mm) than long (6.3mm), gently convex. Radial facets plenary, subhorizontal, narrow gape. Anals 3, in intermediate position. Radianal large, 4.4mm long, 3.8mm wide, in line of radials. Anal X and right tube plate subequal, 2.5mm wide, 2.4mm long, proximal ends barely below radial summit, each adjoining one tube plate distally. IBrr one per ray, wider (9.7mm) than long (5.2mm), slightly convex longitudinally, moderately convex transversely, axillary. IIBrr, IIIBrr, IVBrr and VBrr rectilinear, wider than long, strongly convex transversely, branch on 5th to 8th brachial in each series. First branching isotomous, thereafter heterotomous bi-exotomous, minimum of 10 arms per ray. Pinnules slender, borne by alternating branchials. Stem pentagonal.

REMARKS
The crown was enclosed in a quartz wackestone. It had been crushed slightly by compaction. Irregular calcite cementation of the matrix and hydrous iron oxide cementation and replacement of plate edges along some sutures made preparation difficult.

The specimen is an advanced member of *Texacrinus* with the most elongate slender arms known within the genus. It probably evolved from *T. goochensis* by elongation of the brachials and modification of the anals. It is one of the three youngest known Palaeozoic crinoids.

Texacrinus gascoynensis sp. nov.
(Fig. 17A-D)

ETYMOLOGY
For the Gascoyne River.

MATERIAL
Holotype WAM91.698, from the Artinskian Cundlego or Wandagee Formation on Jimba Jimba Station, Carnarvon Basin. Exact horizon and locality unknown.

DIAGNOSIS
Radial facets peneplenary; anals in a near advanced position with only proximal most tips of anal X and right tube plate below radial summit.

DESCRIPTION
Crown, robust, moderately short, 56.9mm long, average 37.4mm wide, cylindrical. Cup moderate bowl-shaped, large, 10.0mm high, average 33.7mm wide; basal invagination 12.4mm diameter, 4.0mm deep; sutures flush; shagreen ornamentation. IBB 5?, covered, small, confined to basal invagination, probably downflared. BB 5, large, wider (12.9mm) than long (10.0mm), strongly convex longitudinally, mildly convex transversely, forming basal plane of cup; CD basal truncated distally for radianal. RR 5, large, nearly twice as wide (17.6mm) as long (9.0mm), gently convex longitudinally and transversely, mildly outflaring. Radial facets peneplenary with narrow notch, sloping gently outward. Radianal large, slightly wider (8.1mm) than long (7.8mm), adjoined distally by anal x and right tube plate proximal most tips of which are below radial summit. IBrr one per ray, pentagonal, wider

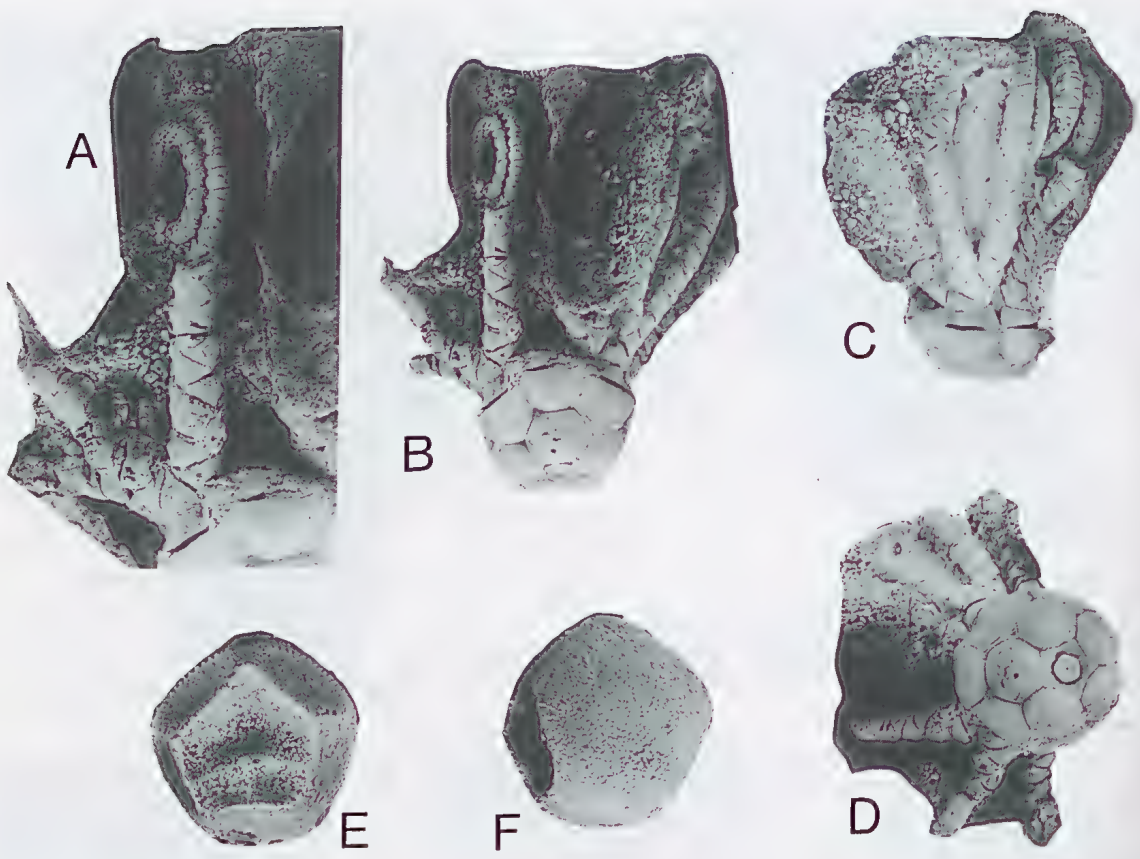


FIG. 20. *Cymbiocrinus cherrabunensis* sp. nov. A, D ray arm showing cuneate brachials, ×1. B-D, posterior, C ray and basal views of holotype CPC30684, ×0.75. E,F, internal and external views of paratype basal QMF21480, ×2.

(14.5mm) than long (6.7mm), constricted distally, strongly convex transversely, gently convex longitudinally, axillary. IIBrr to VIIBrr rectilinear, wider than long, moderately convex transversely, straight to gently convex longitudinally; brachials number 2 IIBr; 3 IIIBr, 4 IVBr, 4 or 5 VBr, 5 VIBr, 3 or 4 VII Br, unknown number of VIII Br. First branching isotomous, all others heterotomous biexotomous; minimum 14 arm per ray. Anal sac unknown, probably short. Stem round transversely, heteromorphic. Latus strongly convex; axial canal round.

REMARKS

This nearly complete crown is replaced with hydrous iron oxides and weathered a deep ferruginus red. It was embedded in a medium-grained quartz wackestone and slightly compressed normal to the A-CD axis. The radial facets are peneplenary and distinguish it within the genus. If the base of the anal X and right tube plate were any higher they would be out of the cup and the form would be considered to have a single anal.

Consideration was given to designating a new genus based on the combination of the peneplenary facets and near single anal condition. Until the single anal condition is established we prefer to retain this form in *Texacrinus*.

Galateacrinus Moore, 1940

TYPE SPECIES

G. stevensi Moore, 1940 from the middle Pennsylvanian Oologah Limestone of Oklahoma; by original designation.

Galateacrinus australis sp. nov.

(Fig. 18A)

ETYMOLOGY

Latin *australis*, southern.

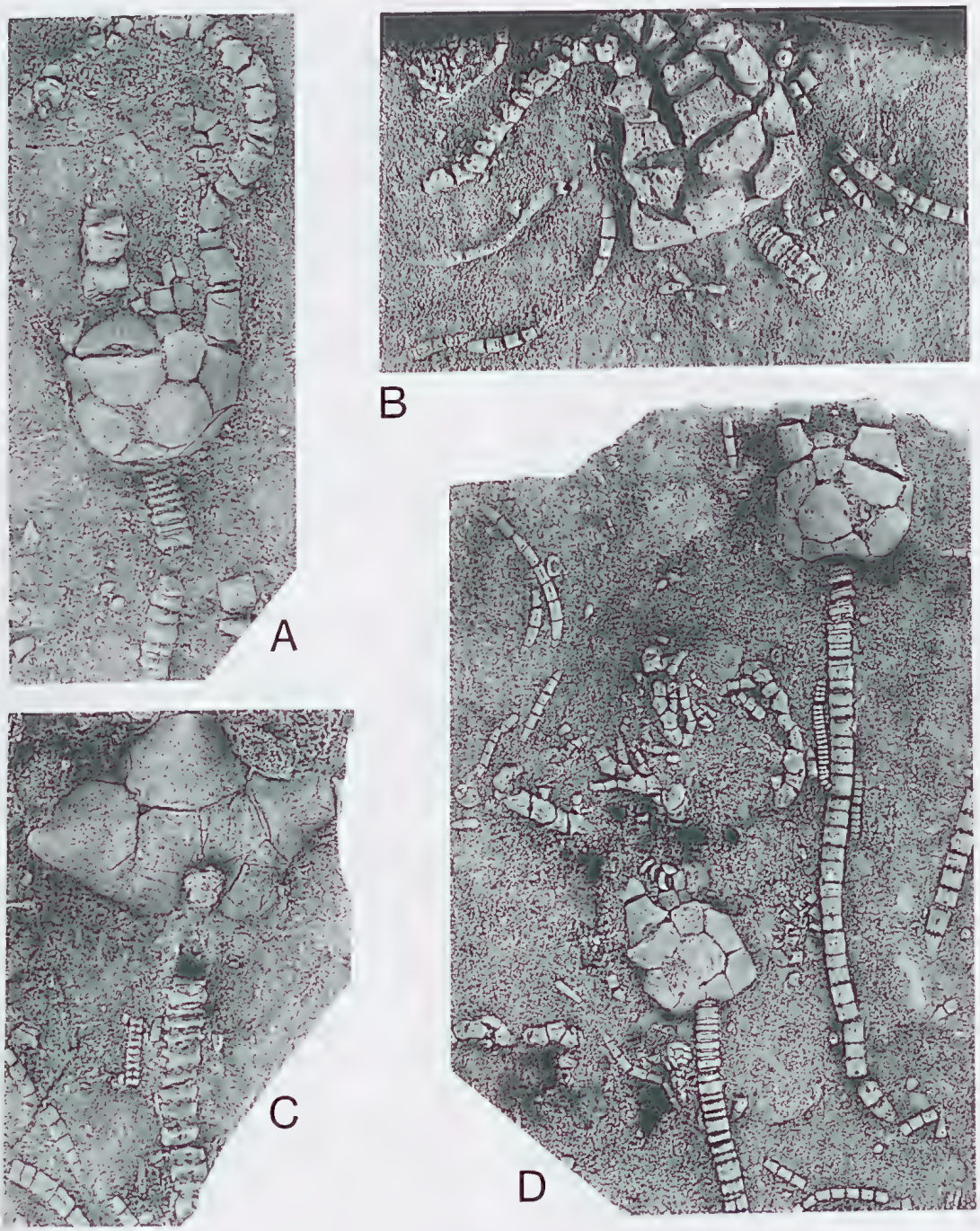


FIG. 21. *Jimbacrinus donnellyensis* sp. nov. A, posterior view of holotype CPC30685, ×4. B, lateral view of weathered paratype crown with arms splayed CPC30690, ×3. C, oblique view of infrabasal circlet and basal invagination of paratype CPC30686 on same slab as A, ×3.5. D, posterior views of paratypes CPC30687 (right) and CPC30688 (left) with *Stomiocrinus merlinleighensis* sp. nov. paratypes CPC30674 (to left of stem, 0.5cm below base of CPC30688) and CPC30675 (extreme bottom right corner), ×3.

MATERIAL
Holotype UWAF113388 from QML770.

DIAGNOSIS
Cup low bowl-shaped, lacking radial notches; brachials very short, locally becoming biserial within the uniserial arms.

DESCRIPTION
Crown tall (85.9mm incomplete) moderately outflaring (55.3mm wide at IBr1), anal sac stout. Dorsal cup low bowl-shape, nearly discoid, twice as wide (33.3mm maximum) as high (16mm diameter); sides widely outflaring; wide deep basal invagination (9.9mm); coarse vermiform(?) ornamentation; sutures weakly impressed. IBB restricted to invagination, probably downflared, not exposed if preserved. BB 5, large, CD 8.8mm long, 10.2mm wide, moderately convex longitudinally, gently convex transversely, proximal ends in basal invagination, widely outflared distally, forming basal plane of cup; CD basal truncated distally for adjoining anal X. RR 5, large, wider (15.5mm) than long (9.6mm), outflared widely; radial facets plenary, sloping strongly outward. Anals 3, primitive arrangement, distal 1/3 of anal X and right tube plate above radial summit. Radianal pentagonal, in oblique position, slightly longer (7.9mm) than wide (6.7mm); adjoining C radial, BC and CD basals, anal X and right tube plate. Anal X hexagonal, longer than wide (8.5x6.2mm), adjoins one tube plate distally. Right tube plate hexagonal(5.5x5.5mm). IBrr 1/ray, wider than long (15.5x6.2mm), moderately convex transversely and longitudinally, axillary. IIBrr to VIBrr strongly convex transversely, wider than long, cuneate with local biserial brachials. First branch isotomous, thereafter heterotomous bi-exotomous. Second branching on IIBrr4 or 5, third through sixth branch on 6th to 8th brachial in the series; 12 arms per ray. Pinnules, anal sac and column not preserved.

REMARKS
Only the C and D rays and adjoining parts of the dorsal cup are exposed and perhaps the only parts preserved. Its lack of radial notches and possession of cuneate brachials leave it transitional between the Texacrinidae (lacking radial notches with rectilinear to cuneate brachials), and the Galateacrinidae (with radial notches and cuneate brachials). The radial notches of the Galateacrinidae are formed by the very bulbous nature of the radials as the facets are actually plenary but adoral of the aboreal tumidity. Thus the Galateacrinidae are separated from the Texacrinidae on the shape of the cup, discoid vs low bowl respectively, not the length of the radial facet as the presence of radial notches tends to imply. We question if this is of sufficient difference to justify family separation.

This is the first record of a *Galateacrinus* in Australia. The genus has previously been reported only from the middle Pennsylvanian to Early Permian of the United States (Webster, 1973, 1977, 1986). The low bowl shaped cup, lack of radial notches and short brachials which locally become biserial readily distinguish *G. australis* from all other species of the genus.

Skaiocrinus Webster, 1990

TYPE SPECIES
Skaiocrinus granulosus Webster, 1990 from the Artinskian Wandagee Formation, Minilya River; by original designation.

Skaiocrinus granulosus Webster, 1990
(Fig. 19)

Skaiocrinus granulosus Webster, 1990:66, pl.2, figs 15-17.

MATERIAL
Cup WAM91.684; 6 partial crowns, WAM91.668, 91.669, 91.671, 91.692, 91.694, 91.696 and 3 sets of arms WAM91.670, 91.691, 91.693 from the Artinskian Wandagee Fmn, Minilya River, collected by H. Coley.

REMARKS
Several morphological features not visible or showing variation not recognisable on the original study material (Webster, 1990) are shown on the new specimens. Cup morphology is quite consistent with the exception of the width of the radial facets. On the holotype they are nearly plenary but must be considered peneplenary, whereas they are plenary or very nearly plenary with slight variation on all new specimens. Arms may branch up to 8 times (WAM91.692), resulting in 9 arms in one half ray and 90 arms for the crown if branching is uniform and maximum in all rays. Pinnules are very slender, taper slightly until the distal termination, have a medial longitudinal ridge, begin on the first secundibrach, and contain 9 plates in proximal pinnules. The slender tegmen is formed of small polygonal plates with flush sutures, no appearant transverse or longitudinal alignment of plates and is recurved. The column is heteromoprhic Type II pattern.

Based on the peneplenary radial facets, Webster (1990) assigned *Skaiocrinus* to the

Pachylocrinidae noting exotomous arm braching and similarity to the Texacrinidae. The genus is here transferred to the Texacrinidae because most of the new specimens show plenary facets.

No formation was known for the original study material. New specimens are from the Wand/agee Formation, in a calcareous siltstone to medium-grained quartz wackestone. Cementation is generally weak but may include hydrous iron oxides which are difficult to remove when preparing specimens. Natural weathering exposed most of the features described above.

Family CYMBIOCRINIDAE Strimple & Watkins, 1969

Cymbiocrinus Kirk, 1944

TYPE SPECIES

Cymbiocrinus romingeri Kirk, 1944 from the early Chesterian St. Genevieve Limestone of Alabama; by original designation.

REMARKS

The Cymbiocrinidae may be divided into 2 groups with differing arm structures *Cymbiocrinus, Aenigmocrinus, Oklahomacrinus* and *Allosocrinus*, have cuneate brachials. *Lecobasicrinus, Aesiocrinus, Paracymbiocrinus* and *Proallosocrinus* have rectilinear brachials. Both groups appear in the Chesterian and range into the Virgilian in the United States. They probably had differing ancestral lineages and may represent different families. Additional investigation of the Cymbiocrinidae is required to properly resolve these problems.

Cymbiocrinus cherrabunensis sp. nov. (Fig. 20)

ETYMOLOGY

For the Cherrabun Member.

MATERIAL

Holotype, CPC30684, a crown from the Tatar-ian Cherrabun Member, Hardman Formation, east side of Mt Hardman, Canning Basin. Coll. J.M.Dickins. Paratype QMF21480 from QML 772.

DIAGNOSIS

Primanal large; 11 arms incurled distally.

DESCRIPTION

Crown 72mm long (arms curled distally), 75mm wide, inflated pear-shaped with incurled distal arms, no surface ornament. Cup medium bowl-shaped, wider (27.3mm) than high (11.8mm), walls outflared, base shallowly invaginated, sutures impressed, moderately deep apical pits. IBB 5, small, kite-shaped, 4.8mm long, 4.7mm wide, downflared, not visible in lateral view of cup. BB 5, large, 10.0mm long, 10.8mm wide, inflated, moderately convex transversely and longitudinally. RR 5, wider (14.3mm) than long (8.8mm), outflared, gently convex transversely and longitudinally. Radial facet plenary, bearing transverse ridge and outer ligament pit, slightly gaped. IBrr two per ray, moderately convex transversely, constricted distally. IBr_1, trapezoidal, wider (14.3mm) than long (3.7mm). IBr_2 triangular, 6.6mm wide 5.3mm long, axillary. All other brachials, unless axillary, strongly cuneate, bearing one slender pinnule each on alternate sides of arm. Arms 11? all branching isotomous. Proximal columnal pentagonal, 4.5mm diameter; latus convex. Crenularium narrow, culmina short, coarse. Areola wide, flat. Axial canal subpentagonal.

REMARKS

Assignment to *Cymbiocrinus* is based on cup shape, single anal, cuneate brachials, and branching on the second primibrachial. A third arm on the C ray (branching on the first secundibrachial abanally) is not typical of the genus. It is uncertain if this represents an evolutionary development or a variant. The bulbous basals show affinity to the calceolispongiid, *Jimbacrinus*, however the calceolispongiids have inflated basals, 5 atomous arms and most commonly a vestigal stem.

Hydrous iron oxides have replaced all plates and the crown is embedded in a coarse-grained quartz wackestone. The delicate arms are incurl-ed distally but visible in the natural weathered specimen. It is interpreted to have lived in or near the burial site on a sandy substrate.

Family TIMORECHINIDAE Jaekel, 1918

Timorechinid gen. indet. (Fig. 18C,D)

MATERIAL

QMF21468 a partial set of arms, QML770.

REMARKS

A small incomplete set of arms (25.0mm long) with 3 series of brachials shows 2 isotomous branchings. Brachials are wider than long proximally, equidimensional medially, longer than wide distally, strongly convex externally, and slightly cuneate. Axillary brachials (5-7 in middle series) have a central upward and outward directed short spine. Most spines are broken off

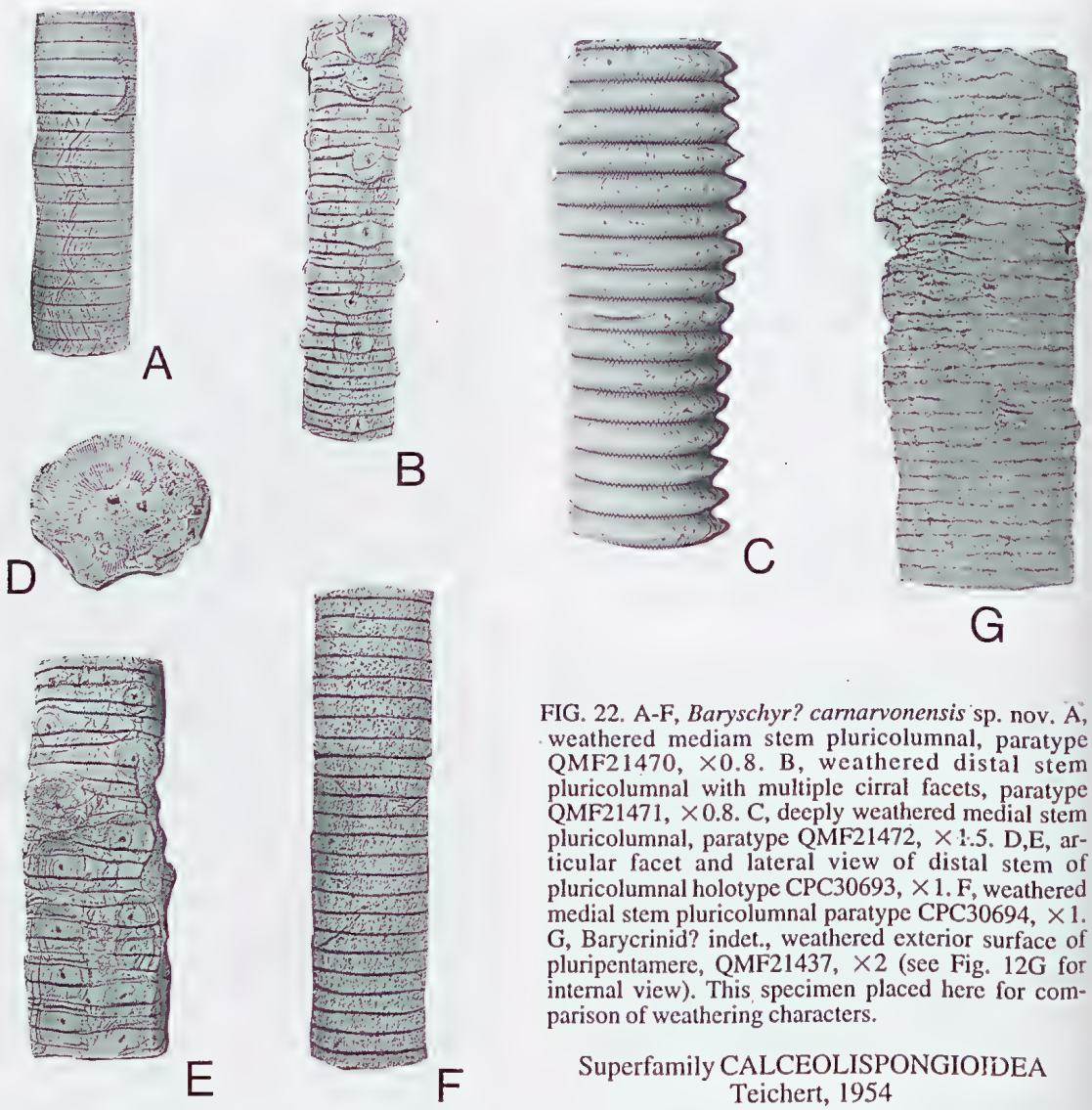


FIG. 22. A-F, *Baryschyr? carnarvonensis* sp. nov. A, weathered mediam stem pluricolumnal, paratype QMF21470, ×0.8. B, weathered distal stem pluricolumnal with multiple cirral facets, paratype QMF21471, ×0.8. C, deeply weathered medial stem pluricolumnal, paratype QMF21472, ×1.5. D,E, articular facet and lateral view of distal stem of pluricolumnal holotype CPC30693, ×1. F, weathered medial stem pluricolumnal paratype CPC30694, ×1. G, Barycrinid? indet., weathered exterior surface of pluripentamere, QMF21437, ×2 (see Fig. 12G for internal view). This specimen placed here for comparison of weathering characters.

and the weathered fracture is sometimes difficult to detect. Isolated spinose axillary brachials probably belonging to this specimen are moderately common at Callytharra Springs. Proximal series of brachials twice width (3.9 mm) of middle series (1.9mm); distal series (1.1 mm wide) >1/2 width of middle series. Except for spines on axils and smaller size, this set of arms is similar to *Notiocrinus timoricus* Wanner (1924a, pl.12, figs 18,19) from Basleo, Timor.

Because the branching pattern cannot be determined and the cup is lacking, the arms are questionably referred to Timorechinidae, with isotomous and heterotomous biendotomous arms.

Superfamily CALCEOLISPONGIOIDEA Teichert, 1954

FamilyCALCEOLISPONGIIDAETeichert,1954

Jimbacrinus Teichert, 1954

TYPE SPECIES

Jimbacrinus bostocki Teichert, 1954 from the Artinskian Cundlego Formation, Western Australia; by original designation.

Jimbacrinus donnellyensis sp. nov.
(Fig. 21)

ETYMOLOGY

For Donnelly's Well.

MATERIAL

Holotype CPC30685, paratypes CPC30686-30691

from the upper part of the Artinskian Bulgadoo Formation in the type section near Donnelly's Well.

DESCRIPTION

Crown small, pear-shaped, arms incurled distally. Cup bowl-shaped, walls subvertical, base slightly invaginated, moderately deep apical pits. IBB 5, kite-shaped, longer than wide, proximally downflared, distally upflared, visible in lateral view of cup. BB 5, hexagonal, subequal to wider than long, proximally subhorizontal, distally upflared becoming subvertical at distal tip; CD basal heptagonal, truncated distally for primanal. RR 5, pentagonal, wider than long, subvertical, bear shallow medial longitudinal depression. Radial facet plenary, bearing transverse ridge, outer ligament pit and marginal shelf. Primanal large, longer than wide, proximal 2/3 in radial circlet, adjoins 2 tegmen plates distally. Arms 5, atomous. Brachials rectilinear proximally, cuneate distally, strongly convex transversely, concave longitudinally, bearing faint longitudinal ridges after 3rd or 4th brachial; IBr_2 bearing two coarse slightly diverging laterally projecting blunt nodes. Pinnules large, elongate, one per brachial on alternate sides of arm. Stem pentagonal in section proximally; latus convex; heteromorphic type 1 pattern; distally round, homeomorphic, bearing few short cirri. Axial canal round.

MEASUREMENTS (mm)

	Holotype CPC30685	Paratype CPC30687	Paratype CPC30686
Crown height	16.7	11.5	
Crown width	12.5*	15.2*	
Cup height	4.1	4.3	
Cup width	6.1	-	
Diameter IBB			7.1
IBB length	1.9*	1.9*	3.4*
IBB width	1.8	1.7	3.1
BB length		2.5	2.2
BB width		3.1	2.2
RR length	2.3	2.0	
RR width	3.1	2.9	
Primanal length	1.8	1.7	
Primanal width	1.6	1.6	
Columnal diameter	1.4	1.4	1.6

*estimated

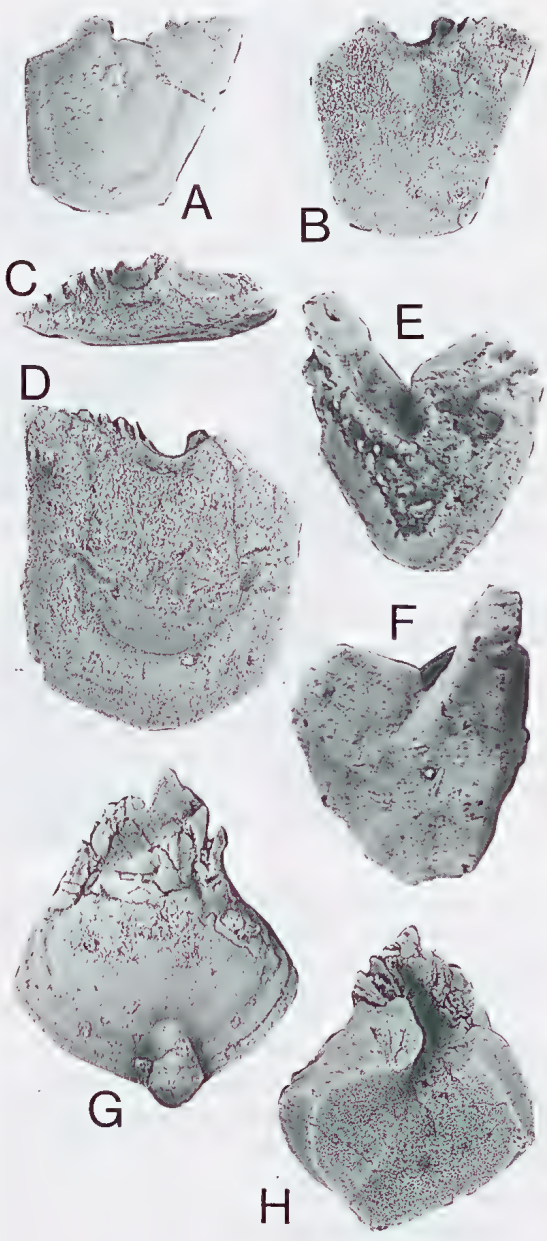


FIG. 23. *Neoschisma verrucosum* Wanner, 1924b. A,B, C radials QMF21481 and 21482, ×10 and ×6, respectively. C,D, oral and lateral views of D radial QMF21483, ×5 and ×6, respectively. E,F, external and internal views of epideltoid QMF21484, ×7. G,H, external and internal views of hypodeltoid QMF21485, ×4.

REMARKS

This description is a composite based on the 7 specimens. The holotype has a well preserved cup, proximal most column and C ray arm but exposed basals have been rounded by solution. One paratype (Fig. 21C) shows the infrabasal circlet and prominent protrusion on the basals. Two specimens (Fig. 21A,B) have well preserved brachials one and two, and two other specimens (Fig.21D) have well preserved columnals showing the gradation from the pentagonal to round sections within approximately one centimeter of the cup. Weathering has etched the surface of most specimens producing nodes and grooves which could be mistaken for ornamentation unless all specimens are considered.

Unlike most species of *Calceolospongia* that rested on the substrate with extended basals (Teichert, 1949), *Jimbacrinus* lived above the substrate supported by the stem (Teichert, 1954). All plates except the basals of *J. donnellyensis* are relatively thin and the crown is small relative to the stem; these features suggest an elevated life habit.

This is the third species of *Jimbacrinus* recognised and it is the oldest. It is easily distinguished from *J. bostocki* and *J. minilyaensis* by the wider basal plane and subhorizontally directed basal protuberances. *J. bostocki* probably evolved from *J. donnellyensis* by development of the central spine on the basals.

Family and genus indet.
(Fig. 18B)

MATERIAL

QMF21469 a partial set of arms from QML770.

REMARKS

This set of arms includes parts of 4 half(?) rays which could be a part or parts of one to three rays. The brachials are: moderately (proximally) to slightly (distally) wider than long; externally strongly convex transversely; bearing a medial longitudinal ridge terminating distally in a very short spine directed upward and outward; and moderately (proximally) to strongly (distally) cuneate. Brachials are slightly offset giving arms a slightly zigzag appearance, which is enhanced by the alternating direction of the medial ridge/spine. Isotomous endotomous or exotomous branching occurs twice on two of the partial rays and possibly a third time on one. A slender pinnule articulates with the branchial at the distal end of the medial ridge aboreal to the spine.

Classification of this specimen is uncertain. The zigzag brachials resemble some genera of the Decadocrinoidea, but they only have 10 arms, isotomously branching on the first or second primibrachial. Four superfamilies of the poteriocrininids include genera with endotomous or exotomous branching. The Hydreionocrinoidea have biserial arms and given no further consideration. The Pirasocrinoidea typically have spine rings capping the anal sac, brachials are rectilinear to faintly cuneate, and few genera are actually known to have endotomous or exotomous branching. *Linocrinus*, *Tholocrinus* and *Exocrinus*, of the Zeacrinitoidea have ray ridges or cuneate brachials but all lack the zigzag offset of the brachials. Only *Linocrinus*, has both ray ridges and cuneate brachials. Cuneate brachials are characteristic to several genera of the Texacrinoidea. *Galateacrinus ornatus* Moore, 1940 has medial ridges terminated in short spines on cuneate brachials, but the brachials are not offset.

Lacking proximal parts of the arms and the cup the specimen is left in open nomenclature. It is illustrated to show recognised diversity in the advanced poteriocrinid faunas from the Callytharra Formation. The branchials and branching pattern are sufficiently distinct to offer correlation potential if similar specimens are found elsewhere.

Family CYCLOMISCHIDAE Moore & Jeffords, 1968

Baryschyr Moore & Jeffords, 1968

Crinoid stem Foord, 1890, p.104, pl.4, fig.11.
Enlarged crinoid stem-portions Etheridge,1903, p.25, pl.4, figs 1-9.

TYPE SPECIES

Baryschyr anosus Moore & Jeffords, 1968 from the Pumpkin Creek Limestone Member, Dornick Hills Formation, Pennsylvanian of Oklahoma; by original designation.

Baryschyr? carnarvonensis sp. nov.
(Fig. 22A-F)

ETMOLOGY

For the Carnarvon Basin.

MATERIAL

Holotype CPC30693, paratypes CPC30694, QMF21470, 21471, 21474 from QML770, QMF21472, 21473 from QML757 and 368 specimens as follows QMF21588 (11 specimens) from QML757, QMF21589 (25) from QML768, QMF21590 (11) from QML769, QMF21591 (201) from QML770, BMRF1643 (28),

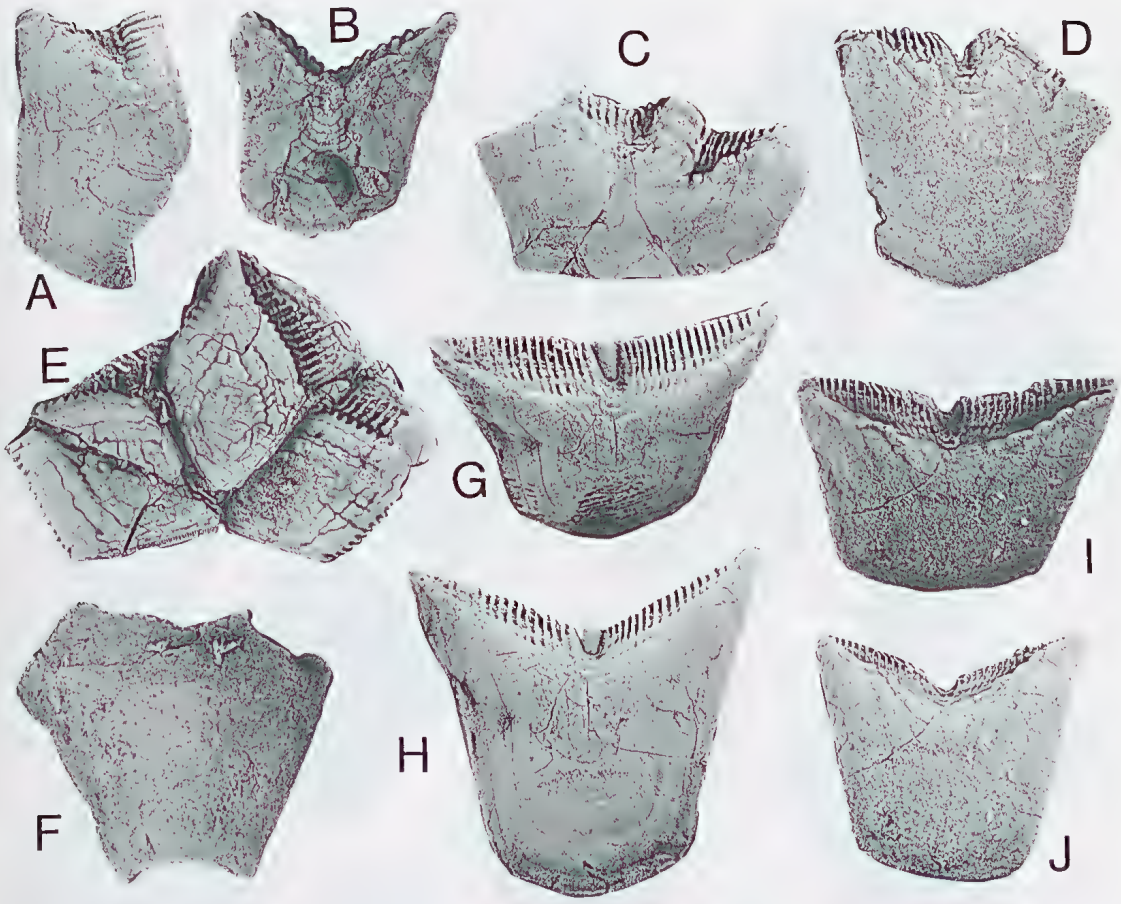


FIG. 24. *Neoschisma extensum* sp. nov. A, fragment of a C radial QMF21486, ×2. B, small radial QMF21487, ×5. C,D, a fragmentary and a complete D radial QMF21488 and 21489, ×3. E, fragmentary articulated theca NMVP127198, ×2.5. F, large basal plate QMF21490, ×2.5. G,H, oblique lateral and lateral views of large radial QMF21491, ×2. I,J, oblique lateral and lateral views of radial QMF21492, ×2.5 and ×2, respectively.

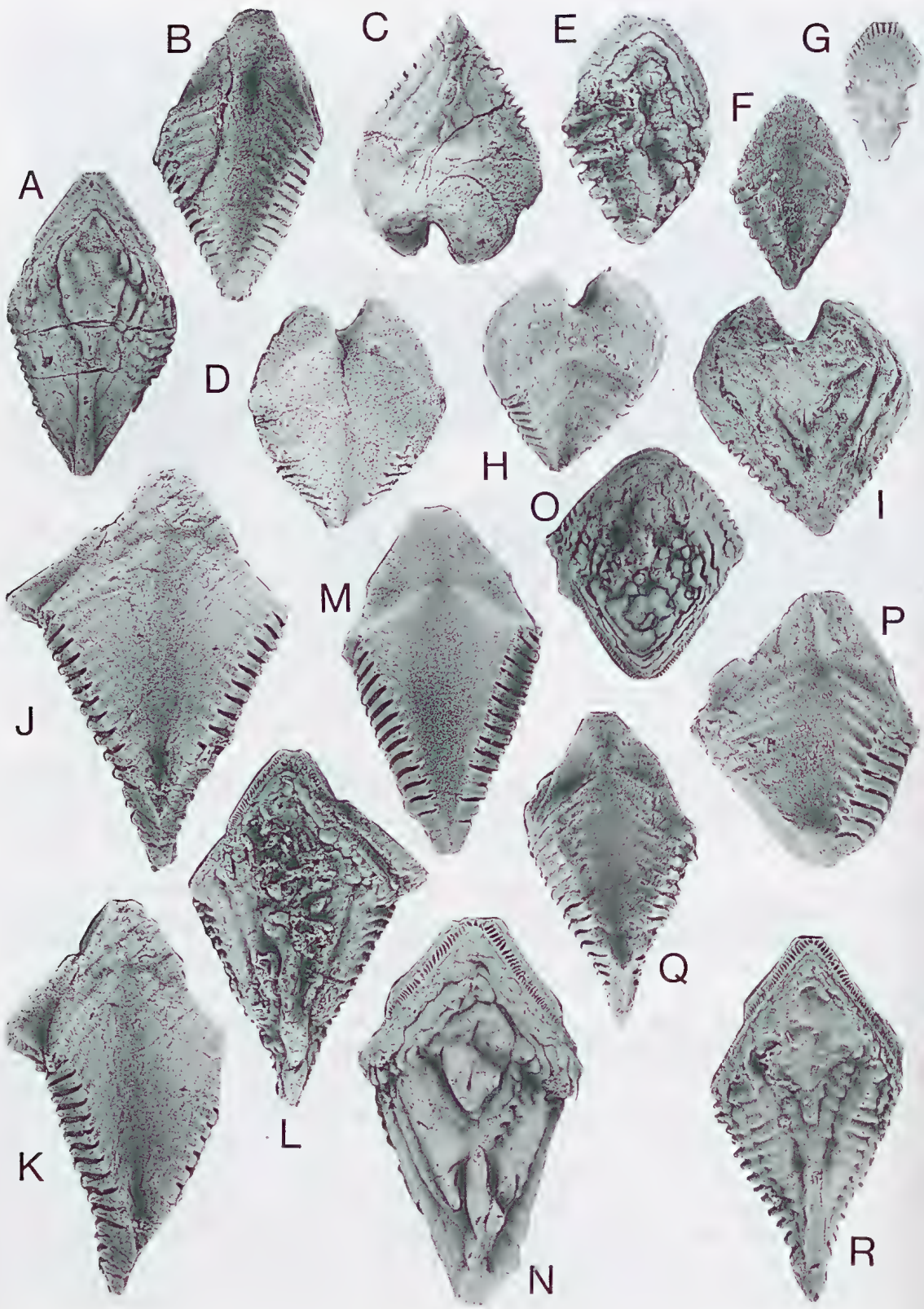
BMRF1644 (5), BMRF17226 (55), BMRF17601 (3), BMRF19385 (4), BMRF19386 (6), BMRCC139 (12), BMRG259 (3)and BMRGW84 (4).

DESCRIPTION

Proximal columnals unknown; medial columnals homeomorphic to heteromorphic type I; cirriferous distal columnals heteromorphic type I. Columnals circular in transverse section, axial canal pentagonal. Articulum wide, full facet width with no areola to nearly full facet width with narrow areola sloping into axial canal. Culmen fine, branching isotomously at midwidth to distal 1/4 of articulum, 40 per cm at mid width of articulum. Symplexy articulation. Latus smooth, straight. Axial canal narrows at moderately convex claustrum on each columnal. Cirri circular in transverse section, articulum like columnal articulum. Cirral scars aligned in part, may give columnal a rough pentagonal section, overlap 1 then 2 adjacent columnals as growth increases; cirri scars increase in size distally.

REMARKS

Large pluricolumnals, 5.0-9.4cm long and 1.7-2.4cm diameter are especially common in exposures of the basal part of the Callytharra Formation throughout the Carnarvon Basin. They have been collected for many years and are present in most major museum collections throughout Australia. The first illustrations of these columnals was by Foord (1890) followed by Etheridge (1903) who reported infestations of endophytic fungus on some stem segments. More recently Welsh (1976) has demonstrated that these infestations and others referred to myzostomids by Warn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(1974), among others, are caused by *Phosphannulus*.

Considerable morphologic and diagenetic variation occurs in the pluricolumnals of *B.? carnarvonensis*. Many pluricolumnals lack cirri whereas others have a few and others many. Those with cirri show a progradation of increasing size of the facet distally and a corresponding alignment of the facet and more pentagonal transverse section of the columnals with the larger facet sizes. Heteromorphic noditaxial patterns change distally. Proximal patterns are 2 or 3 internodals between nodals in fairly regular repetitions. Distally internodals are fewer and occur infrequently, one every 3 to 7 nodals. The distal irregular noditaxis patterns correspond to the most cirriferous pluricolumnals.

Weathering of the pluricolumnals is greatest along articular facets resulting in pluricolumnals with a V-shaped or cog-shaped latus and what appears to be impressed sutures. Weathering on some specimens has been deep and results in irregularly shaped transverse cross-sections. The large axial canal collapsed under compaction after burial and many pluricolumnals appear elliptical in transverse section.

Class BLASTOIDEA

The only descriptions of Western Australian Permian blastoids have been those of Breimer & Macurda (1972) who named the fissiculates *Neoschisma australe* and *Notoblastus stellaris* and identified the Timorese species *Thaumatoblastus lonigramus* Wanner, 1924b in Western Australia and Breimer (1983) where the detailed species descriptions were provided. Apart from providing further information on each of these a new spiraculate species is described and the Timorese species *Neoschisma verruscosum* is recorded in W.A. Apart from this specific match all have generic links to Timor suggesting a close biogeographical link between the two areas.

Order FISSICULATA Jaekel, 1921
Family NEOSCHISMATIDAE Wanner, 1940

Breimer & Macurda (1972) discussed fissiculate phylogeny in great detail having established their classification apparently phenetically. All the fissiculates described herein are assigned to the Neoschismatidae following Breimer & Macurda. The only comment regarding intergeneric relationships concerns the placement of *Pterotoblastus*. Although placed in the Codasteridae by Wanner (1940) and by Breimer & Macurda (1972) *Pterotoblastus* appears to have quite a deal in common with various neoschismatids, in particular *Notoblastus*. The major distinguishing feature appears to be the reduction in the number of slits per hydrospire field and loss of slits on the anal deltoid in *Pterotoblastus*. Breimer & Macurda (1972) made an emphatic point that "Hydrospire structures of neoschismatids are essentially unchanged; ... There is no trend towards reduction in the number of hydrospire slits, neither in regular, nor in anal hydrospire groups". However, their further discussion of hydrospires in the Family reveals an abundance of slits in the earliest representative, *Hadroblastus*, and several of the Permian genera but in several species, effective reductions are recorded. According to Breimer & Macurada (1972, p. 346) these reductions are effected through filling of the slits by secondary calcite deposits. They regard *Timoroblastus* as a form with most of its slits completely closed off by secondary calcite. *Pterotoblastus* has more slits than *Timoroblastus* and the small number in each genus could be due to the same process, calcite infilling of most slits. In the anal interray groups of slits, *Neoschisma* contains one species with approximately the same number of slits as non-anal groups because the hypodeltoid bears numerous slits; a second species has a greatly reduced number where the hypodeltoid does not bear slits. In *Notoblastus* there are 1-5 slits in each anal hydrospire field. This is significantly fewer than in anal fields of certain species in other genera where slits are present on both epi- and hypodeltoids. Even in *Notoblastus*, *N. cornutus* (McKellar, 1969) has 5 slits per group in the D interray, *N. oyensi* (Wanner, 1940) and *N. stellaris* have 3 and *N. brevispinus* has 2. Therefore, we consider that the difference between 2 and 0 slits in the anal group no more significant than that between 5 and 3. We suggest that *Pterotoblastus*

FIG. 25. *Neoschisma extensum* sp. nov. A,B, external and internal views of deltoid QMF21493, ×4. C,D, external and internal views of holotype hypodeltoid QMF21494, ×4. E,F, external and internal views of small deltoid QMF21495, ×7 and ×6, respectively. G, external view of small deltoid QMF21496, ×6. H,I, internal and external views of hypodeltoid QMF21497, ×4. J-L, internal, internal oblique and external views of large deltoid with lancet still attached QMF21498, ×4. M,N, internal and external views of large deltoid QMF21499, ×4. O,P, external and internal views of deltoid QMF21500, ×4 and ×5. Q,R, internal and external views of deltoid QMF21501, ×4.

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may be more correctly classified with the essentially Permian Southern Hemisphere group, the Neoschismatidae.

Neoschisma Wanner, 1924b

TYPE SPECIES

N. verrucosum Wanner, 1924b from the Permian of Timor; by original designation.

Neoschisma verrucosum Wanner, 1924b (Fig. 23)

Neoschisma verrucosum Wanner, 1924b:7, pl. 199, figs 9,10.
Neoschisma verrucosum Wanner; Breimer & Macurda, 1972:31, pl.19, fig.5; pl.20, fig.7.
Neoschisma australe Breimer & Macurda, 1972:31, pl.19, figs 6,7. [non figs 1-4, 8].
Neoschisma verrucosum Wanner;Breimer, 1983: 126, pl.26, figs 5,7,9.
Neoschisma australe Breimer & Macurda; Macurda, 1983: pl.27, fig. 2 (only); pl.28, figs 7-9, 12.

MATERIAL

Western Australia – UMMP58682 (holotype of *N. australe*) from the type section of the Callytharra Formation, 0.88 km west of Callytharra Springs, WA. QMF21485 an hypodeltoid, QMF21484 an epideltoid and QMF21481-21483 radials from QML757.

DISCUSSION

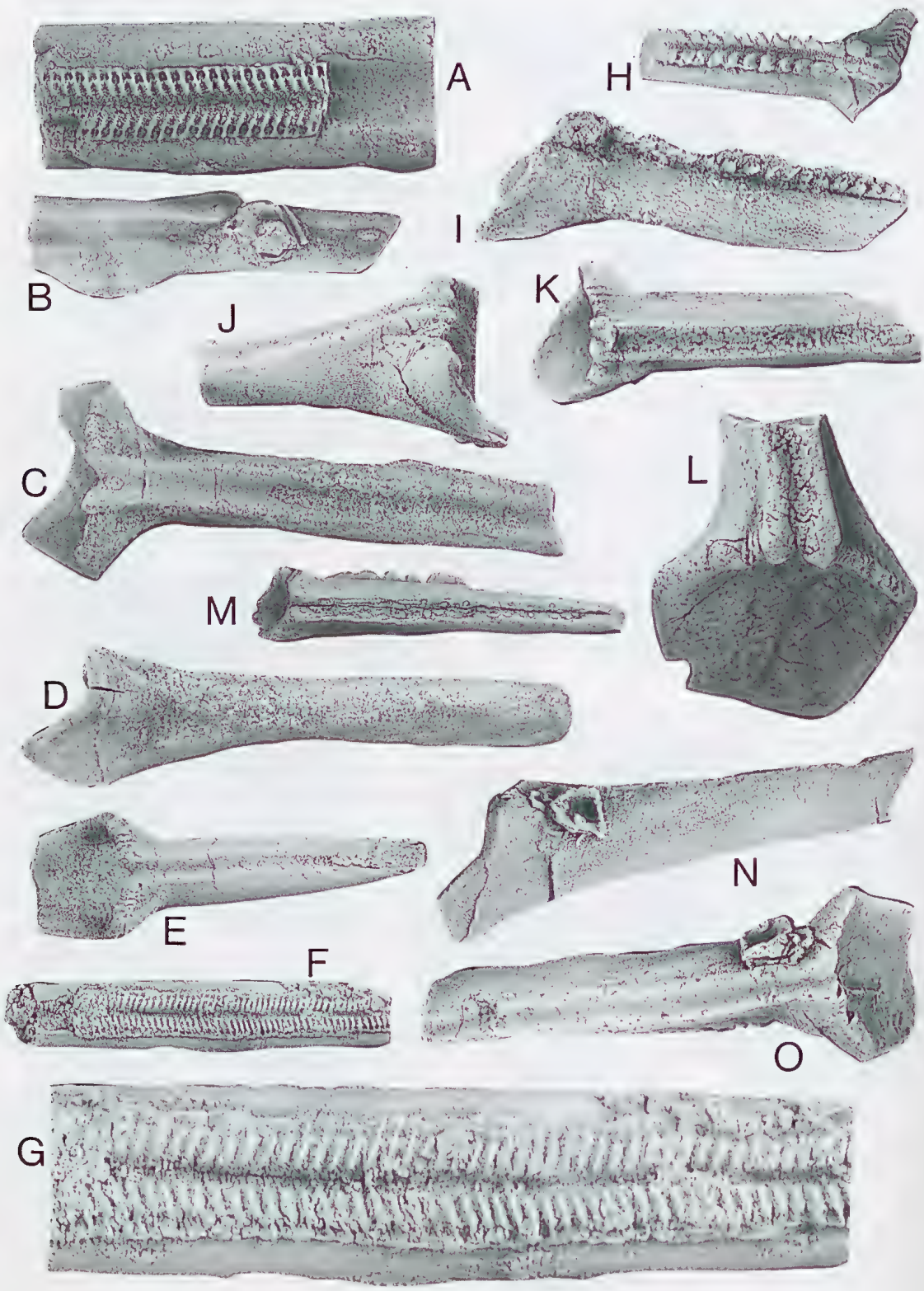
Breimer & Macurda (1972) diagnosed *N. australe* as having a flat rather than scalloped vault and as having hydrospire slits developed on both the epi- and hypodeltoids. The surface of the vault was a variable feature in the Callytharra collections with the depth of the V in the top of the radials and the convexity of the deltoids varying with growth and among individuals of similar size. With the relatively few specimens available this feature would seem unsuitable for species separation. However, development of hydrospire slits on both epi- and hypodeltoids should be clear cut. In the type species, the hypodeltoid does not bear any hydrospire slits (Wanner, 1924b, pl. 199, fig. 10; Breimer & Macurda, 1972, pl. 19, fig. 5). In the holotype of *N. australe* (Breimer & Macurda, 1972, pl. 19, figs 6, 7) the hypodeltoid is a flat, fairly upright plate, tapering adorally but not pointed, with the anal aperture an indistinct invagination into the adoral side and with a distinct double tubercle medially on the aboral RD margin.

Another such plate (Fig.23G,H) is now available with the same shape, distinctive aboral tubercle and ragged adoral margin. In this specimen the protruding ragged adoral edge conceals the anal aperture which is obvious on the internal side. The anal opening cuts through a prominent curving ridge that runs across the plate. A low but distinct ridge runs from near the centre of this gap to the RD margin towards the C side. Moreover this specimen bears no hydrospire slits. On this basis we assign the holotype of *N. australe* and the isolated hypodeltoid mentioned above to *N. verrucosum* based on the lack of hydrospire slits on the hypodeltoid. Radials (2 C and 1 D radials; Fig.23A-D) with truncated upper corners are referable to this species also; the truncation corresponds to the RD margin along the hypodeltoid.

On the other hand, the hypodeltoid figured by Breimer & Macurda (1972, pl. 19, fig. 1) and two others (Fig. 25C,D,H,I) do bear numerous hydrospire slits. These plates represent a separate species and are described below. To that species are also assigned several radials which may be identified as having the "broad convex humped area" described by Breimer & Macurda (1972, p.32) in the hydrospire field adjacent to the hypodeltoid near its widest point. However, many radials, basals and deltoids, from other than the anal part of the theca are not able to be assigned with certainty. They are here assigned to *N. extensum* for convenience only.

The epideltoid (Fig.23E,F) is assigned to this species because the anal opening is irregular, anal collar very low and there are hydrospire slits on both its aboral extremities. Despite the considerable size difference between this epideltoid and available hypodeltoids it seems to fit with the hypodeltoid described above in that the low collar

FIG. 26. *Notoblastus stellaris* Breimer and Macurda, 1972. A-D, external views of deltoids QMF21502-21505. A,B, ×7; C,D ×6. E, oral view of small radial QMF21506, ×4. F,G, lateral and oral views of small radial QMF21507, ×4. H,I, oral views of radials CPC30967 and QMF21508, ×3 and ×5, respectively. J,K, lateral views of small radials QMF21509 and 21510, ×4. L-N, oral view of epideltoids QMF21511-21513. L,M ×5; N ×7. O,P, internal and external views of lancet QMF21514, ×7 and ×10. Q, external view of lancet QMF21515, ×10. R, internal view of lancet QMF21516, ×9. S,T, oral and lateral oblique views of fragment of a radial with lancet still in place CPC30695, ×4. U, fragmentary radial and lancet QMF21517, ×6. V, fragmentary radial CPC30966, ×3. W,X, oral and lateral views of articulated but badly weathered theca NMVP127199, ×2.5. Y,Z, lateral and oral views of large radial QMF21518, ×3.5.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and irregular opening would fit better with the overhanging anal opening described above.

Neoschisma extensum sp. nov.
(Figs 24,25)

Neoschisma australe Breimer & Macurda, 1972:31, pl.19, figs 1-4, 8.
Neoschisma australe Breimer & Macurda; Breimer, 1983:122, pl.27, figs 1, 3-12; pl.28, figs 1-6, ?10, 11, 13-16; pl.30, fig.3.

ETYMOLOGY
Latin *extensus*, stretched out; referring to the anal collar.

MATERIAL
Holotype QMF21494, an hypodeltoid from QML760. Paratypes hypodeltoid and D radial (Breimer & Macurda, 1972, pl. 19, fig. 1), C radial (Breimer & Macurda, 1972, p. 19, fig. 3, 4; BMR GW137), D radial (Breimer & Macruda, 1972, pl. 19, fig. 8) NMVP127198 an articulated but crushed and incomplete theca from 20.3m in the type section of the Callytharra Formation, 0.88km west of Callytharra Springs. QMF21490 fragmentary basal, QMF21486-21489, 21491, 21492 almost complete radials, QMF21493, 21495, 21498-21501 deltoids, hypodeltoid QMF21497 from QML757. One deltoid, QMF21496 from QML760.

DISCUSSION
The problem of assigning non-anal plates to *N. verrucosum* or this new species has been discussed above as has the hypodeltoid with hydrospire slits belonging to the new species. One hypodeltoid (Fig.25C,D) is of the same maximum width as the isolated hypodeltoid of *N. verrucosum* (Fig.23G,H) so the different hypodeltoids may not be attributed to different growth stages of the same species. Any isolated plates of *Neoschisma* that cannot be definitely referred to one or other of the species is tentatively referred to this new species.

The description of *N. australe* as given by Breimer & Macurda (1972, p. 32) and Macurda (1983, p.122) should be applied to this new species except as varied in the following. The fragmentary basals suggest that the BB sides of the plates diverged strongly adorally to give the theca a strongly flared base. In large radials, lateral edges are not always straight; often having a gently sigmoidal curve over adoral half (Fig.24H). In C and D radials hydrospire slits are absent in a zone near to and on the anal interarea side of the central and ambulacral notch. This zone was described by Breimer & Macurda (1972) as that where a "broad convex humped area formed". In specimens available to us (Fig.24A,C,D) the convexity is at right angles to the hydrospire slits and parallel to the RD margin with sharp furrows crossing the humped area also parallel to RD margin (Breimer & Macurda, 1972, pl.19, fig.4; Fig.24A). The upper margin of this convex zone is in contact with a convex face on the hypodeltoid just adoral to the hydrospire slits. On the interior side of this convex area on the radial is a shallow concave channel that leads across the RD suture along the deltoid to the anal opening. Lateral to this convex zone on the radial, the projection of the radial limb is greatly reduced and in one specimen the hydrospire field is declined aborally (Fig.24D). In this same CD interarea position there appears to be a greater than normal development of secondary calcite in front of the slits and one specimen (Fig.24D) a shield has grown almost completely hiding the slits from lateral view.

One available deltoid (Fig.25O,P) is much shorter, in interradial direction, than other deltoids. This specimen has the aboral tip slightly downturned forming a shallow aboral pocket on the internal surface. It has 8 hydrospire slits on one

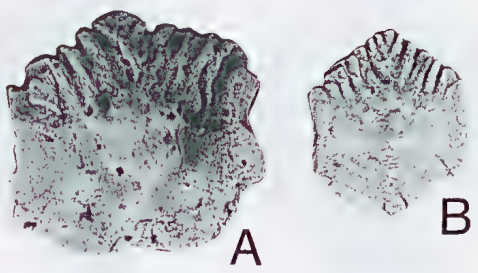
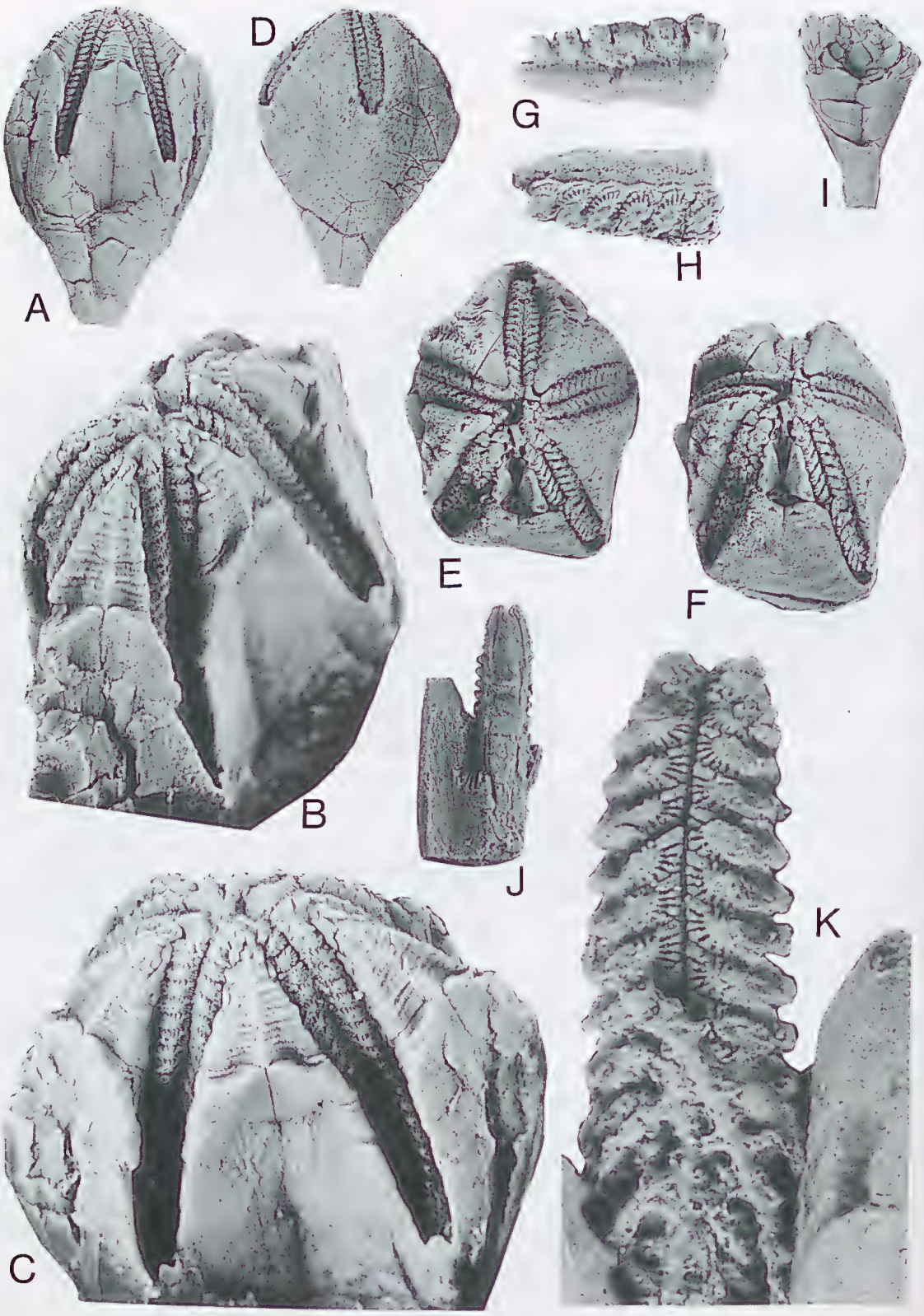


FIG. 28. Deltoid indet. A, CPC30710, x4. B, QMF21553, x3.

FIG. 27. A,F,G, *Thaumatoblastus* sp. nov. fragments of radial projection from KNF73. A, CPC30698, ×5. F,G, CPC30702, ×3 and ×7.5, respectively. B-E, J-O, *Thaumatoblastus* indet. B-E from KNF73; J-O from ML89. B, fragment of radial projection showing branched ambulacral tract, CPC30699, ×3. C,D, oral and lateral views of radial with incomplete projection, CPC30700, ×3.5. E, radial, CPC30701, ×4. J-M, radials with incomplete projections, CPC30705, 30706, 30707, 30708, respectively, ×2.5, ×3, ×3, ×4, respectively. N,O, lateral and oral views of radial with incomplete projection and upon which a juvenile mollusc shell (probably an oyster) has attached, CPC30709, ×2.5. H,I, *Thaumatoblastus longiramus* Wanner, 1924b, radials with incomplete projections but retaining the lancet and side plates, CPC30703, ×4 and CPC30704, ×3.


A
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C

side and only 3 or 4 on the other, whereas elongate deltoids of comparable width may have 15 or 16 slits. The side with only 3 or 4 slits has a long aboral zone without slits. Whether this is from an aberrant specimen or there is some other explanation is not known at present. We have no epideltoid to assign to this species. The two hypodeltoids appear dissimilar principally because one has a very high anal collar, subdued comarginal ornament and prominent distal blade-like projection whereas the other has no raised anal collar, prominent sharp comarginal ridges and no distal projection. On the latter specimen the anal collar and distal projection may have bene removed by postmortem abrasion. Internally (Fig.25D,H) the two plates are identical with a ridge across the plate at the adoral end of the hydrospire slits. On the surface of the anal groove, adoral to the transverse ridge, are low irregularly placed tubercles. Adorally on the plate are a pair of flat facets presumably for junction with the epideltoid.

One deltoid retains a lancet on one side (Fig.25J-L) and one radial retains the short aboral tip of the lancet in the ambulacral notch (Fig.24G,H). The DD margin of the deltoid is straight adorally, then slightly concave and convex dipping down aborally. This shape is well illustrated in the assembly of Breimer & Macurda (1972, pl.19, fig.1) but the dorsal half of deltoids should be in contact. In oral view the lancet corresponds to this shape being narrow and depressed adorally beneath the abutting deltoids, but wider and flush, with the sides of the deltoids in the main body area where deltoids do not touch. In Breimer & Macurda's (1972, p.33) description it is not clear which part of the lancet is being referred to as adoral and which is aboral; in this work the adoral section is where the ambulacral groove is supported entirely by the deltoids, the main body is where the ambulacral groove is supported by the lancet and adoral section is on the radial. The lancet is widest at aboral end of main body, tapering very slowly adorally it disappears internally at adoral end of the main body. Small transverse grooves are evident within the ambulacral tract but the arrangement of side plates or even their presence is not confirmed by available material.

Notoblatus Brown, 1942

TYPE SPECIES

Notoblastus brevispinus Brown, 1942 from the Early Permian of New South Wales; by original designation.

Notoblastus stellaris Breimer &Macurda, 1972 (Fig. 26)

Notoblastus stellaris Breimer & Macurda, 1972:34, pl.20, fig. 1; pl.21, figs 1,2,7,8.

Notoblastus stellaris Breimer & Macurda; Breimer, 1983:132, pl.29, figs 5-7,11,12; pl.30, figs 1,2,4-10,15-17.

MATERIAL

Holotype UMMP58683 from the type section of the Callytharra Limestone on the Wooramel River, WA. NMVP127199 an articulated but weathered specimen from locality BB929 which is 20.2m above the base of Section 7 on Mt. Sandiman Station, 1.9km at 15° from Mt Sandiman Woolshed, from the collection of Dr G.A. Thomas, now housed in the Museum of Victoria. Radials QMF21506-21510, 21517, 21518, CPC30965, 30967, deltoids QMF21502-21505, epideltoids QMF21511-21513, and lancets QMF21514-21516 from QML757.

DISCUSSION

This species was described in detail by Breimer and Macurda (1972:34) and Macurda (1983:132); only where new information is available are comments added here. However, an attempt is made to illustrate several features and plates not obvious in earlier papers.

The theca described here is taller than that of Breimer & Macurda (1972) with the basals accounting for some 25-30% of total height; the height is 17mm and maximum width 16mm but this theca is compressed laterally so the width is overstated. In life the theca must have been considerably higher than wide.

On the radials, the ambulacral sinus extends along the radial projection to the point where the projection turns upwards; in the smaller specimens this means the sinus does not extend onto the projection at all but in the largest radial (Fig.26Y,Z) the sinus extends well out onto the projection to the point where the upper surface of the projection is about to turn upwards. There

FIG. 29. *Rhopaloblastus cuspidus* sp. nov. A-C, lateral, oral oblique and lateral oblique views of holotype theca QMF21519, A ×3; B,C ×7. D-F, lateral, oral and posterior oblique views of paratype theca NMVP94182. D ×3; E,F ×4.5. G,H, lateral and oral views of fragment of a lancet with 6 side plates attached QMF21520, ×10. I, basal circlet of small theca QMF21521, ×3. J,K, internal and external views of a lancet still in place on a radial QMF21522, ×4 and ×15.

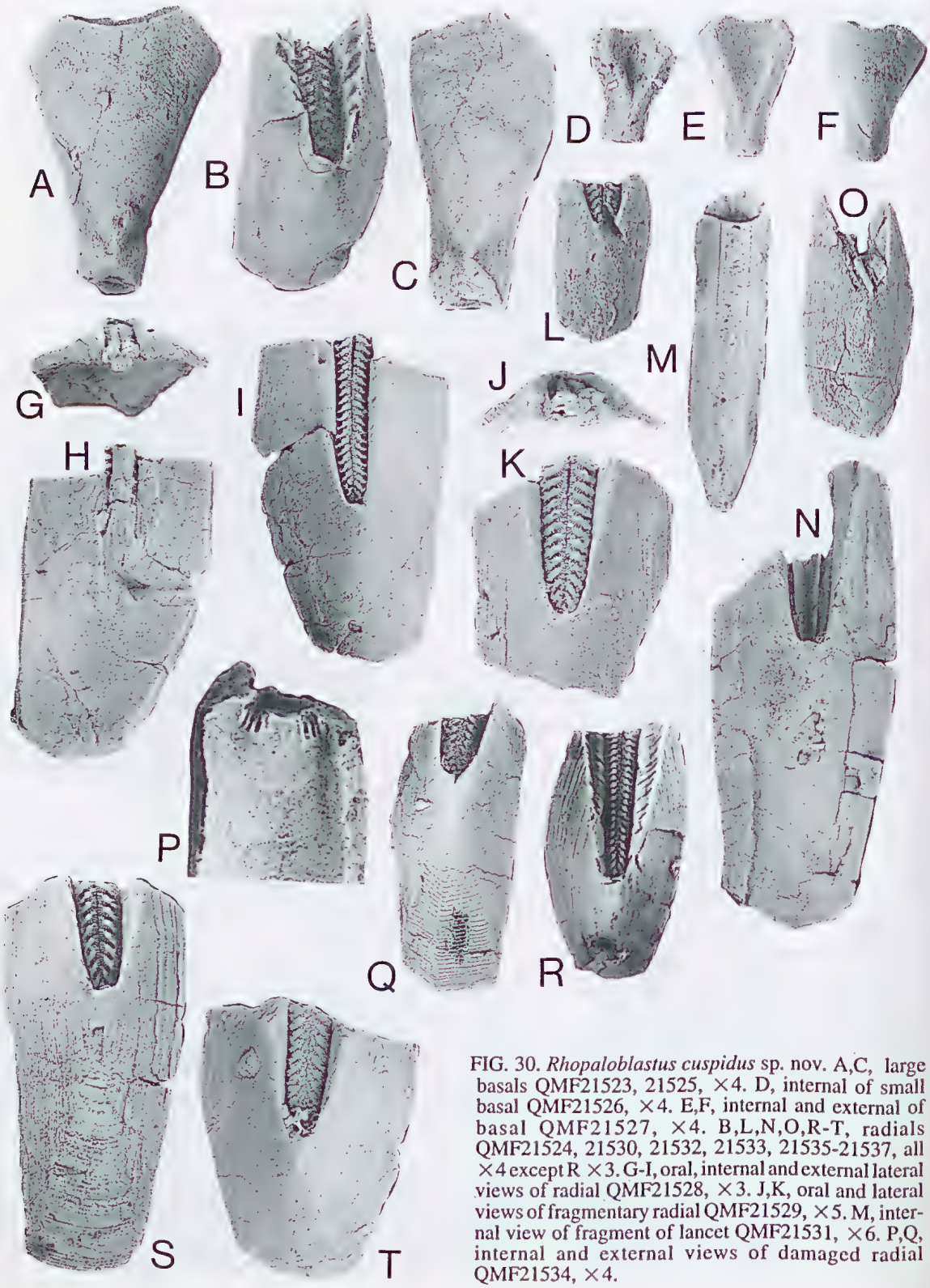


FIG. 30. *Rhopaloblastus cuspidus* sp. nov. A,C, large basals QMF21523, 21525, ×4. D, internal of small basal QMF21526, ×4. E,F, internal and external of basal QMF21527, ×4. B,L,N,O,R-T, radials QMF21524, 21530, 21532, 21533, 21535-21537, all ×4 except R ×3. G-I, oral, internal and external lateral views of radial QMF21528, ×3. J,K, oral and lateral views of fragmentary radial QMF21529, ×5. M, internal view of fragment of lancet QMF21531, ×6. P,Q, internal and external views of damaged radial QMF21534, ×4.

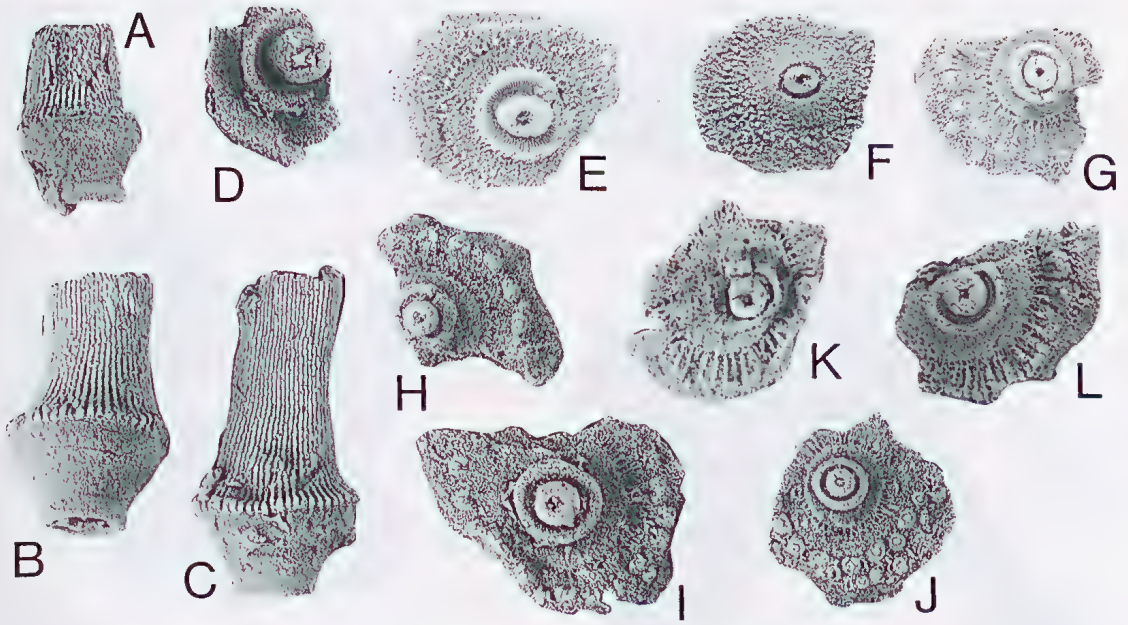


FIG. 31. Cidaroid indet. A-C, spine bases QMF21541-21543, ×4. D-L, fragmentary interambulacrals QMF21544-21550, all ×7 except E and I ×6.

appears to be some variation in the shape of radials through growth but the small sample size and degree of postmortem deformation make it impossible to identify how much. In the CD interray, hydrospire slits are reduced to one or two per field and these situated close to the ambulacrum. In the smaller radials described here, both in the articulated specimen and as disassociated plates, the hydrospire fields are not evident in lateral view; although the individual plates all appear to have undergone a degree of distortion this is unlikely to have accounted for the attitude of the hydrospire fields in every case. In large radials (Fig.26S,U,Y,Z) the hydrospire fields are more upright and evident in lateral view.

Epideltoid same as a deltoid except that hydrospire fields are reduced to 1 or 2 slits on each margin projection at lateral extremes; these projections were sutured to radials. On inner sides of these projections are elongate facets that presumably sutured to the hypodeltoid. In the centre of the plate was a large circular anal opening. The adorally chevron-shaped ridge of the deltoid is greatly accentuated. No plate in our collections may be certainly identified as the hypodeltoid but its shape is inferred from the epideltoid and radial that would have bounded it. The hypodeltoid must have been wide and rhomboidal with the adoral corner excavated by the anal opening so that a shape approaching broadly arcuate is possible.

Since isolated lancets and those still in the ambulacra of weathered radials (Fig.26S,U) show the lancet to be elongate rhomboidal in plan view. The adoral part (i.e. from widest point to adoral tip) is shorter than aboral part which tapers very gently and extends to tip of ambulacrum. Laterally on adoral part are the slightly protruding faces that abut the excavation into the sides of the deltoids. On internal surface is an adoral diamond shaped area bounded by a distinct ridge and with concave surface. The aboral tip of the diamond fills the V-shaped gap in the radial and the aboral extension with rounded inner surface lies in the ambulacral groove on the radial.

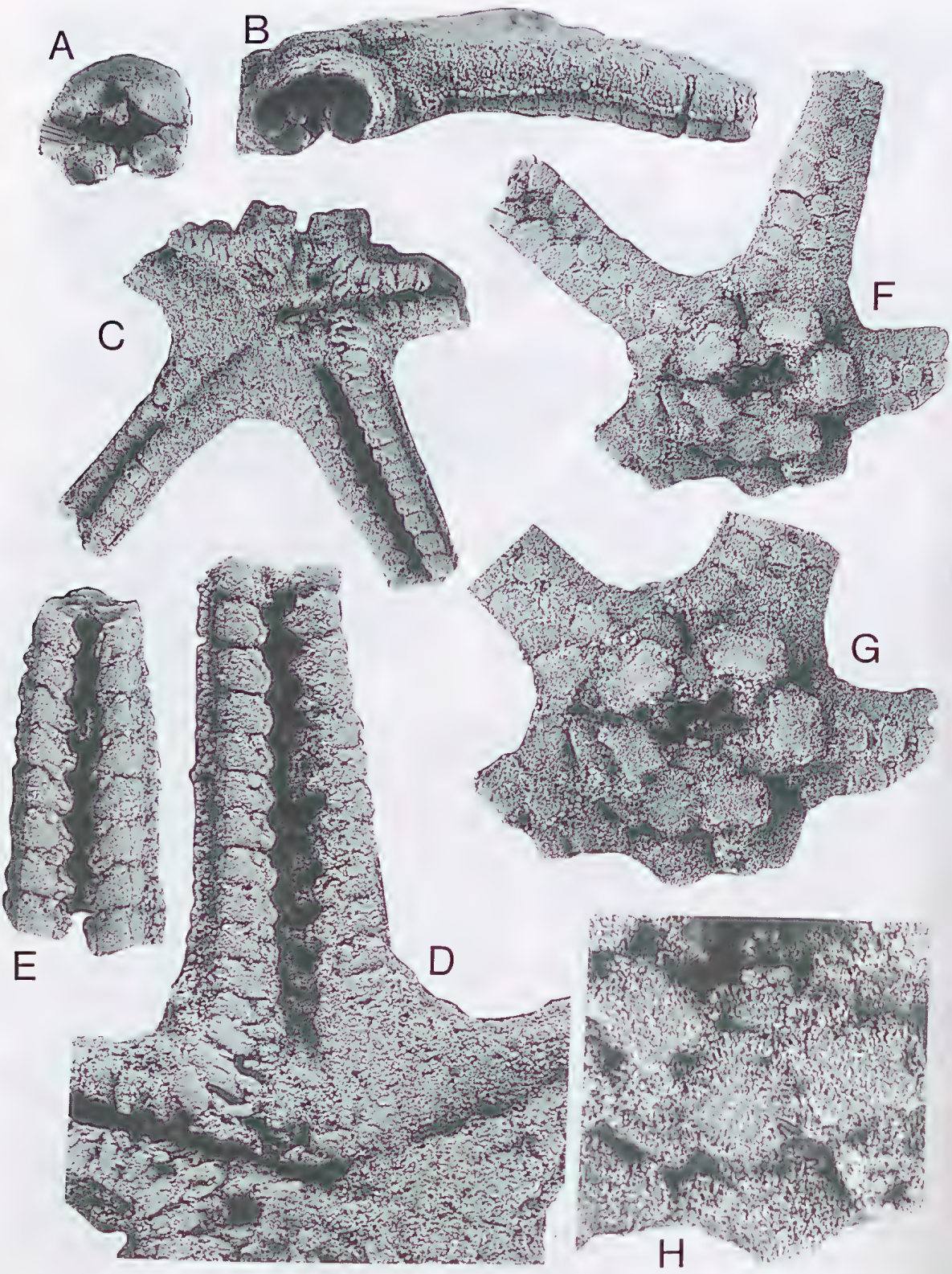
Thaumatoblastus Wanner,1924b

TYPE SPECIES

Thaumatoblastus longiramus Wanner,1924b from the Permian of Timor; by original designation.

Thaumatoblastus longiramus Wanner,1924b (Fig.30H,I)

Thaumatoblastus longiramus Wanner:Breimer & Macurda, 1972:36, pl.24, fig.2; pl.25, figs 1-8; pl.28, fig.5.


A
B
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H

Thaumatoblastus longiramus Wanner: Macurda, 1983:135, pl. 31, figs 7-10; pl.32, figs 1-10.

MATERIAL
Radial plates CPC30703, 30704 from ML87.

REMARKS
One of these radials (Fig.27H) was figured by Breimer & Macurda (1972, pl.25, fig.5) and agrees with the other in size of the side plates relative to the width of the ambulacrum. These side plates appear to be the same size and shape as figured by Wanner (1924b) and their assignment to the type species is accepted.

Thaumatoblastus sp. nov.
(Fig.27A,G)

MATERIAL
Radial plates CPC30698,30702 from KNF73 and QMF30705-30709 from ML89.

REMARKS
The two specimens with lancet and side plates preserved (Fig.27A,F,G) show a greater number of side plates per centimetre of ambulacrum when compared with the 2 radials described above as *Thaumatoblastus longiramus*. These two specimens are considered specifically separate but because they are so incomplete no new specific name is introduced.

Thaumatoblastus sp. indet.
(Fig.27B-F,J-O)

MATERIAL
Radial plates CPC30699-30701 from KNF73 and QMF30705-30709 from ML89.

REMARKS
Assignment of these radials, that have lost their lancet and side plates, to either of the species mentioned above is not possible with the present state of knowledge. However, it is likely that they belong to one or other of the species occurring in Western Australia. All those radials figured by Breimer & Macurda (1972, pl.24, fig.2; pl.25, figs 1-4, 6,8; pl.28, fig.5) which do not retain a lancet or side plates are in the same situation and definite specific assignment will depend on more detailed study of this and better material from Western Australia and Timor if and when it becomes available.

Family UNCERTAIN
Deltoid indet
(Fig. 28)

MATERIAL
Two plates QMF21553 from QML757 and CPC30710 from 20m above base of the type section of the Callytharra Formation.

DESCRIPTION
These two plates are hexagonal with the six sides virtually of equal length. Two adjacent sides have 7 or 8 slits normal to the margin; interpreted as hydrospire slits. Comarginal growth lines are evident parallel to the other sides; a group of 6-9 low rounded tubercles are situated centrally with the central tubercle highest and most prominent.

REMARKS
Although these plates are abraded and only one is preserved so as to be confident of its features they are interpreted as the deltoid plates of some blastoid because of the hydrospire slits and general resemblance to the deltoids of *Notoblastus* described above. However, the six even sides to these plates and apparently unspecialised edges (ie. other than those with slits) are features unknown among the blastoids. Their identity even as blastoid plates, remains a mystery at present but they are recorded to show the diversity.

Order SPIRACULATA Jackel, 1921
Family PENTREMITIDAE d'Orbigny, 1851

Rhopaloblastus Wanner, 1924b

TYPE SPECIES
R. timoricus Wanner, 1924b from the Permian of Timor; by orginal designation.

DIAGNOSIS
See Breimer & Macurda,1965:216.

REMARKS
Breimer & Macurda (1965) considered *Rhopaloblastus* to differ from other genera in the Pentremitidae by its petaloid ambulacra and exposed cryptodeltoids. The species described below has exposed cryptodeltoids but ambulacra,

FIG. 32. *Monaster coleyi* sp. nov. A,E, adoral end and oral view of arm fragment (could be part of holotype but not certain) NMVP127201, ×7 and ×8, respectively. B-D, F-H, holotype NMVP127200. B, lateral view of A ray, ×5. C,D, oral view, ×4 and ×7. F,E, aboral view, ×4 and ×6. G, enlargement of madreporite area, ×10.

in the largest available specimen, are not petaloid but rather elongate, much more in the style of *Calycoblastus*. We have assigned the species with the emphasis on the anal deltoid arrangement because that feature seems generically more consistent through the blastoids. The smaller theca (Fig.29D,E) exhibits more petaloid ambulacra but in all other respects this species coincides better with the type of *Calycoblastus* than *Rhopaloblastus*. *Calycoblastus* was originally protrayed (Wanner,1924b) as having eight spiracles and an anispiracle. Brown (1942) credited *C. casei* from New South Wales with 10 spiracles. However, Breimer & Macurda (1965) re-examined the holotype of the type species arguing from the weathered surface that it possessed four spiracles and an anispiracle. This is in accord with the diagnosis of *Rhopaloblastus* and with the species described below but *C. casei* Brown, 1942 has yet to be re-examined to verify this feature and determine whether it should remain in that genus. Radials of this new species closely resemble radials ascribed to *Rhopaloblastus* (?) *belfordi* (Crockford & Brown) (Brown,1942:102) from the Permian of the Hunter Valley and to *Rhopaloblastus*? cf. *belfordi* (McKellar,1969:25) from the Berserker Beds near Rockhampton. Without knowledge of the anal deltoids it is impossible to assign these isolated radials generically; their elongate ambulacra indicate *Calycoblastus* but the similarity to those assigned to *Rhopaloblastus* below suggest the earlier assignments may be correct. It is surprising that no reference was made to *Calycoblastus* in discussions of these eastern Australian radials by either author.

Rhopaloblastus cuspidus sp. nov.
(Figs 29,30)

ETYMOLOGY

Latin *cuspis*, point; refers to adoral projection of radial at centre of ambulacra.

MATERIAL

Holotype QMF21519; paratypes articulated specimens QMF21519, 21521, and NMVP94182, basals QMF21523, 21525-21527, radials QMF21524, 21528-21530, 21532-21537, and lancets QMF21520, 21522, 21531 from QML757.

DESCRIPTION

Calyx tall, with height to width ratio 2, maximum width at aboral extremities of ambulacra which are 0.3 of height from oral pole; vault dome-shaped. Pelvis conical, with relatively broad base (2mm), at least at calical height of about 20mm. Stem unknown.

Basals three, approximately half pelvic height, each occupying 120° of circumference, slightly waisted just above stem attachment, with straight flaring sides; upper margin concave to chevron-shaped centrally, descending on both sides. Stem attachment area terminal, flat to gently concave, with narrow marginal crenullarium. Radials tall, occupying about half calical height, with well developed comarginal growth ridges in each growth sector, externally convex in both transverse and vertical section, with broad low tubercle at origin a short distance below the aboral end of ambulacral sinus, with a low ridge extending over that short distance and the ridge waisted at its midlength. As the ridge widens towards the ambulacrum it merges with a narrow smooth area of secondary calcite deposition bordering the ambulacral sinus under which growth lines of the RR sector simply disappear. At the aboral end of the ambulacral sinus a short broad cusp projects orally (often broken off on available material but if not evident, the broken base is evident). Ambulacral sinus of variable length but usually occupying about half length of radial (almost all dissociated radials are broken in the RD sector, making it impossible to be certain of this proportion but in some radials the length of the RB sector relative to its width suggests that the ambulacral sinus may occupy less than 20% of radial length). Ambulacra narrow, widening only gently adorally, depressed beneath outer surface of radial; lateral walls of ambulacral sinus becoming higher towards RD front, gently convex, crossed at low angle to lateral margins by growth ridges that are coarser than on the exterior, sigmoidal in section with variable attitude from almost vertical and then the sigmoidal section only weakly evident to much lower angle exposing a stronger sigmoidal section and producing a much wider ambulacral sinus; in the latter case the groove formed by the sigmoidal wall of the sinus is closer to the external surface than the convex roll and the groove does not reach the aboral end of the sinus. On the floor of the ridges is a further groove to accommodate the lancet plate; lancet extremely long, subquadrate in section, covered by side plates. Side plates each with single large prominent brachiolar facet and hydrospire pore abradially between successive side plates; side plates in contact along radial line throughout ambulacrum. RD margin variably transverse to chevron-shaped orally, and either straight or slightly sigmoidal, overlying part of deltoid; some isolated radials appear to have

pointed limbs suggesting the RD margin could, in that case, be rather short but articulated specimens of that type are unknown. On the radial interior secondary calcite near the aboral end of the ambulacrum has weathered away in some specimens exposing the hydrospires in groups of 5.

Deltoid with tall triangular aboral part bearing a median radial crest and prominent transverse coarse growth ridges that run aborally down the wall of the ambulacral sinus; oral end expanded into large deltoid lip around the spiracle opening which descends at a low angle beneath the triangular part of the deltoid. Around the spiracle and extending down the deltoid-ambulacrum boundary are small upright spiracle cover plates. Anal deltoid area destroyed by compaction in holotype but a superdeltoid is evident with low ridged radial ornament on it in a dislocated situation. On paratype theca (Fig.29E,F) the exposed cryptodeltoids are evident with weathered remnants of the hypodeltoid also apparent. Oral opening pentagonal.

REMARKS

The complete holotype and paratype (Fig.29D-F) provide most of the critical information on arrangement of plates in the theca. In the holotype, features may not be directly interpreted because of compaction after death which has apparently shortened the polar axis and probably increased its diameter. Most isolated plates available are incomplete or crushed but all in all a fairly good idea of the species is available.

This species is distinguished by its thecal and ambulacral shapes and has the unique feature of the cusp in the aboral end of the ambulacral sinus. The prominent growth lines across the deltoid also appear to be distinctive.

Class ECHINOIDEA
Subclass REGULARIA Latreille, 1825
Order CIDAROIDA Claus, 1880

Cidaroid indet.
(Fig.31)

MATERIAL

Spine bases QMF21541-21543 and fragmentary interambulacral plates QMF21544-21552 all from the type section of the Callythara Formation (QML761).

REMARKS

Teichert (1951:80) reported that echinoids are quite unknown in the Permian of Western Australia and none have been described since then. In washed samples from the type locality of the Callytharra Formation fragments of echinoids have been found and are reported here to make the faunal list more comprehensive.

The primary tubercles on these interambulacral plates are typically cidaroid with their prominent boss, platform, and tubercle.The noncrenulate tubercles along with the long, solid spines with longitudinal ridges suggest the Archaeocidaridae but the Miocidariidae cannot be excluded so family assignment is not attempted. Although different stages of weathering could be inducing different appearances of the plate ornament away from the tubercles it seems highly likely that at least 2 different types are present. Therefore, the possibility should be kept in mind that more than one species is present.

Archaeocidaris selwyni Etheridge,1892 from the Permian of NSW so the group is known from Australia but that species had much larger interambulacral plates than are available from the Western Australian sample. Although these species are probably closely related useful comparison is not possible at present.

Class STELLAROIDEA Lamarck, 1801
Family MONASTERIDAE Schuchert,

Monaster Etheridge,1892

TYPE SPECIES

Palaeaster clarki deKoninck, 1877 from the Permian of New South Wales; designated Schuchert,1914.

Monaster coleyi sp. nov.
(Fig.32)

ETYMOLOGY

For the collector Mr J. Coley who was bookkeeper at Wandagee Station for many years.

MATERIAL

Holotype NMVP127200 and paratype NMVP127201 from the Wandagee Beds (horizon q-r), on the north bank of the Minilya River in the eastern limb of the syncline near Coolkilya Pool. Collected by J. Coley. From the collections of C. Teichert deposited in the University of Melbourne and transferred to the Museum of Victoria in the early 1980s.

DESCRIPTION

This species is described by comparison with *Monaster wandageensis* Kesling,1969.

Stellate; arms tapering gradually to nearly parallel-sided; widened adorally to produce smooth curve on the interbrachial margin. Disc with prominent coronet on aboral surface; R1 subrec-

tangular, smooth, lying over Sm2 plates and abutting Sm1 plates on adpolar corners. Plating inside Sm1 circlet unknown. Interradially and distally between Sm2 plates is a deep cleft. M large, overlapping two Sm2 and abutting two R1 plates, with subradial striae.

Oral surface flat, mouth small; Adm1 and Ax not clear.

Arms strongly plated. Amb plates small, set deep in ambulacral groove. Admm wider than long, with transversely oblique row of 3 or 4 short stout spines, with obtusely pointed margin on ambulacral groove, with abradial margin in zone of tiny plates apparently part of a shagreenate skin covering the aboral surface and terminating at the junction between Imm and Admm.

Imm longer than Admm, approximately subquadrate, with obtusely pointed adradial margin, with series of transverse flutings along abradial edge. Radials small, subquadrate proximally, becoming more rounded distally, not in contact with each other, in contact with Imm at certain points only leaving gaps at sutures between Admm. All covered by finely shagreenate skin with small plates embedded in it.

REMARKS

This species is separated from the closely related *M. wandageensis* Kesling,1969 from the same locality by its nontuberculate R1, smaller Sm1, interradial clefts between Sm2 plates, and finely shagreenate aboral skin. It differs from *M. carnarvonensis* Kesling, 1969 also from the same locality, by the subrectangular R1, larger M, less tapering arms and finely shagreenate skin. It differs from the type species in the narrower, and straighter arms and more numerous arm plates.

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LOCALITY REGISTER

QML localities are in the Callytharra Formation. Map sheets referred to are in the 1:250 000 Geological Series.

QML757 – North side of bladed track from Callytharra Homestead to Byro Homestead in western most exposures 1.5km west of type section south of Wooramel River. 25°52'30"S, 115°29'E Wooramel Sheet SG50-5, 1966.

QML758 – North side of bladed track from Callytharra Homestead to Byro Homestead as track enters dry wash tributary to Wooramel River; lowermost fossiliferous shale and marl capped by limestone in lower fossiliferous unit in Callytharra Formation. type section. 25° 52'30"S, 115° 30'05"E, Glen burgh Sheet SG50-6, 1963.

QML759 – Second fossiliferous shale and marl capped by limestone in type section. South side of track and stratigraphically higher than QML758.

QML760 – Third fossiliferous shale and marl capped by limestone in type section. Immediately south of and stratigraphically higher than QML759.

QML761 – Fourth and fifth fossiliferous shale and marl capped by limestone in type section. Immediately south and stratigraphically higher than QML760.

QML767 – Flats south of low hill approximately 100-150m northeast of turnoff to Merlinleigh Homestead, 6.5km west northwest of Mt Sandiman Homestead. 24° 23'S, 115° 20'E, Kennedy Range Sheet SG50-1, 1963.

QML768 – Flats with low limestone exposures 50-100m east of new road to Moogoorie on both sides of northeast-southwest fenceline, 24° 18'57"S, 115° 18'40"E, Kennedy Range Sheet SG50-1, 1963.

QML770 – 2-3km east of Mundarrie Well in limestones of west dipping hogbacks north and south of Carnarvon-Lyndon road; GR292356, Winning Pool - Minilya Sheet SF50-13, 49-16, 1984.

QML771 – Third massive sandstone above base of Wandagee Formation, 50-150m north of Minilya River in east limb of syncline; GR257375, Winning Pool-Minilya Sheet SF50-13, 49-16, 1984.

QML772 – Bench in lower slope below cliff 0.5-1.0km NNW of type section in Cherrabun Member of

Hardman Formation, Millyit Range; GR767877 Crossland Sheet SE51-16, 1977.

BMRloc. KNF73 – Noonkanbah Formation (type section) at Brutens Yard.

BMR loc. ML87 and ML89 – Bulgadoo Shale, lowermost fossiliferous horizon; campsite east of Mia Mia Homestead. 23° 21'S, 114°34'E.

A NESTING COMMUNITY OF FALSE WATER RATS *XEROMYS MYOIDES* ON THE MYORA SEDGELANDS, NORTH STRADBROKE ISLAND.

Memoirs of the Queensland Museum 32(1): 374. 1992:- The False Water Rat *Xeromys myoides* Thomas, 1889 was described from Mackay. There are 14 in museums: 8 Northern Territory (1, from Sth Alligator R. [Parker, 1973]; 2, Daly R. [Redhead & McKean, 1975]; 2, Tomkinson R. [Magnusson et al., 1976]; 3 Melville Is. [Magnusson et al. 1976]): 6 Queensland (3, from Mackay [Thomas, 1889 (holotype), McDougall, 1944 (5, 3 have been lost)]; 1, Beerwah [Dwyer et al., 1979]; 1, Bribie Is. [Qld Museum JM2381]; 1, Nth Stradbroke Is. [Van Dyck, 1979]). In addition, specimens have been sighted or trapped-and-released: N.T. - Tomkinson R., 4, and Melville Is. where 3 were captured from an extraordinary mud nest (Magnusson *et al.*, 1976); Qld - Proserpine, 2 (P. Campbell, pers. comm. 1981), Kinaba Is., 1, Cooloola, 1, and Beerwah, 1 (Dwyer et al., 1979).

This small species has been seen and collected in or near shallow coastal wetlands such as mangrove forests, freshwater lagoons, swamps and sedged lakes close to foredunes. Little is known of its ecology or social behaviour. Curiously, it is not even known if the False Water Rat is aquatic.

This note reports the recent discovery of a number of active nests of *X. myoides* in the Myora sedgelands, North Stradbroke Is., (see Van Dyck, 1992). On 2 November, 1991, a large, reed-covered mound similar to that described by Magnusson et al. (1976) was found 13m inland from the upper mangrove limit on the Myora sedgelands, between Capembah and Cooroonpah Cks (27°27'58"S,153°25'47"E). Overnight trapping at the mound was unsuccessful. The following day a two hour survey along this narrow sedge strip revealed 3 more nests at intervals of 80-410m. Overnight trapping at one of these nests yielded an adult female (HB:120mm, TV:87mm, HF(su):24, E(n):14.4mm, W:49g) which was photographed, fitted with a radio transmitter and released at the capture site. This individual had small white spots over the dorsum, posterior of the shoulder blades. Similar spots were evident in JM2381 collected at Myora Springs in 1978. On 15 November, 1991, a 6hr survey of coastal sedgeland between Myora Springs and Chiggil Chiggil found another 8 possible nests that varied from relatively simple tunnels built into the supralittoral bank to more complex mounds. A recently constructed mound was found near Myora Springs on 4 February, 1992.

All mounds were located within the narrow ribbon of reed and sedgeland (1.2m high) where salinity is reduced by freshwater drainage. This zone, comprised almost exclusively of *Juncus kraussii*, *Baumea juncea*, *B. rubiginosa* and *Fimbristilis ferruginea* was up to 30m wide and was sharply delineated from the upper mangrove woodland tract (*Avicennia marina*, *Rhizophora stylosa* and *Bruguiera gymnorrhiza*) and the lowest extent of the wallum (dominated by *Melaleuca quinquenervia*, *Eucalyptus intermedia*, *E. robusta*, *Leptospermum liversidgei*, *Gahnia sieberiana* and *Caustis blakei*). Mounds were built on slightly elevated 'islands', some being found among small patches of stunted *Melaleuca quinquenervia* and *Casuarina glauca*, others on raised sedge hummocks. One nest was incorporated around the stem of a living *Vitex trifolia* var. *bicolor*.

Mounds were from 20cm to 60cm high with basal circumferences from 1.6m to 4.8m. From 1 to 3 entrance holes were found at each mound but others may have been hidden under the labyrinth of exposed tree roots into which mounds were often incorporated. These holes were oval in shape (approximately 60mm by 40mm) and were positioned either at the top or the bottom of mounds; they were from 30cm to 2m apart. Although lower holes were flooded at high tide, the mounds themselves were never entirely inundated.

Evidence of external mound 'workings' consisted of fresh roof plasterings in which a thin paste of black mud mixed with peat, dried leaves, sedges, or crab shell had been daubed over the top of the mound and worked between sedges (usually *Juncus kraussii*). Areas 'plastered' in this way measured as much as 1200cm^2 and fresh 'plastering' seemed to indicate that the nest was occupied.

X. myoides has been variously described as 'one of the rarest of our native mammals', 'vulnerable to changes caused by man', 'rare, scattered (probably at risk in some habitats and extinct in others)' and I designated it as 'vulnerable' (Van Dyck, 1991). It is not known whether the few records of the species reflect genuine rarity or a lack of searching effort in appropriate habitats. However, an occupied band of mud nests of *X. myoides* in the Myora sedgeland provides an excellent opportunity for future conservation research.

The commitment of the Endangered Species Program (ANPWS) to funding such research is gratefully acknowledged. Dr Peter Bostock (Queensland Herbarium) provided plant identifications.

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Steve Van Dyck, Queensland Museum, PO Box 3300, South Brisbane 4101, Queensland, Australia; Ellie Durbidge, Point Lookout, North Stradbroke Island 4183, Queensland, Australia; 17 February, 1992.

THE AUSTRALIAN ASCIDIACEA PART 3, APLOUSOBRANCHIA (2)

PATRICIA KOTT

Kott, P. 1992 10 01: The Australian Ascidiacea Part 3, Aplousobranchia (2). *Memoirs of the Queensland Museum* **32**(2): 375–620. Brisbane. ISSN 0079-8835.

In this continuing systematic revision of the taxonomy of the class Ascidiacea (subphylum Tunicata) taxa in the formerly polyphyletic family Polyclinidae Milne Edwards are treated. Included are all species recorded from Australian waters with a posterior abdomen containing the gonads, and usually the heart. New families are erected to accommodate the genera formerly grouped in the polyphyletic Euherdmaniinae, viz. Placentelidae (*Placentela*), Protopolyclinidae (*Protopolyclinum*, *Monniotus*, *Condominium* n.gen.), Ritterellidae (*Ritterella*, *Dumus*, *Pharyngodicyton*), Euherdmaniidae (*Euherdmania*) and Pseudodistomidae (*Pseudodistoma*, *Anadistoma* n.gen., *Citorclinum*). The family Polyclinidae is redefined and restricted to the genera formerly comprising the nominal subfamily Polyclininae, viz. *Polyclinum*, *Aplidiopsis*, *Sidneioides*, *Synoicum*, *Morchellium* and *Aplidium*.

Larvae, observed for the majority of species, have characters significant at species, genus and family levels, and constitute valuable evidence of phylogenetic affinities. Embryos are incubated to tailed larvae internally in all taxa, usually being fertilised and beginning their development in the distal part of the oviduct, sometimes in a brood pouch constricted off from the zooid and sometimes at the base of the oviduct.

Colony development is significant in this group of aplousobranch taxa in which replication is prolific. Zooids are arranged in various colonial, including cloacal, systems. In taxa with extensive cloacal spaces (*Aplidium*), and in those with a soft test (e.g. *Polyclinum*), intracolonial hydrostatic pressure appears to contribute to colony turgidity. Sand and other inclusions in the test add strength and contribute to diversity in colony size and shape.

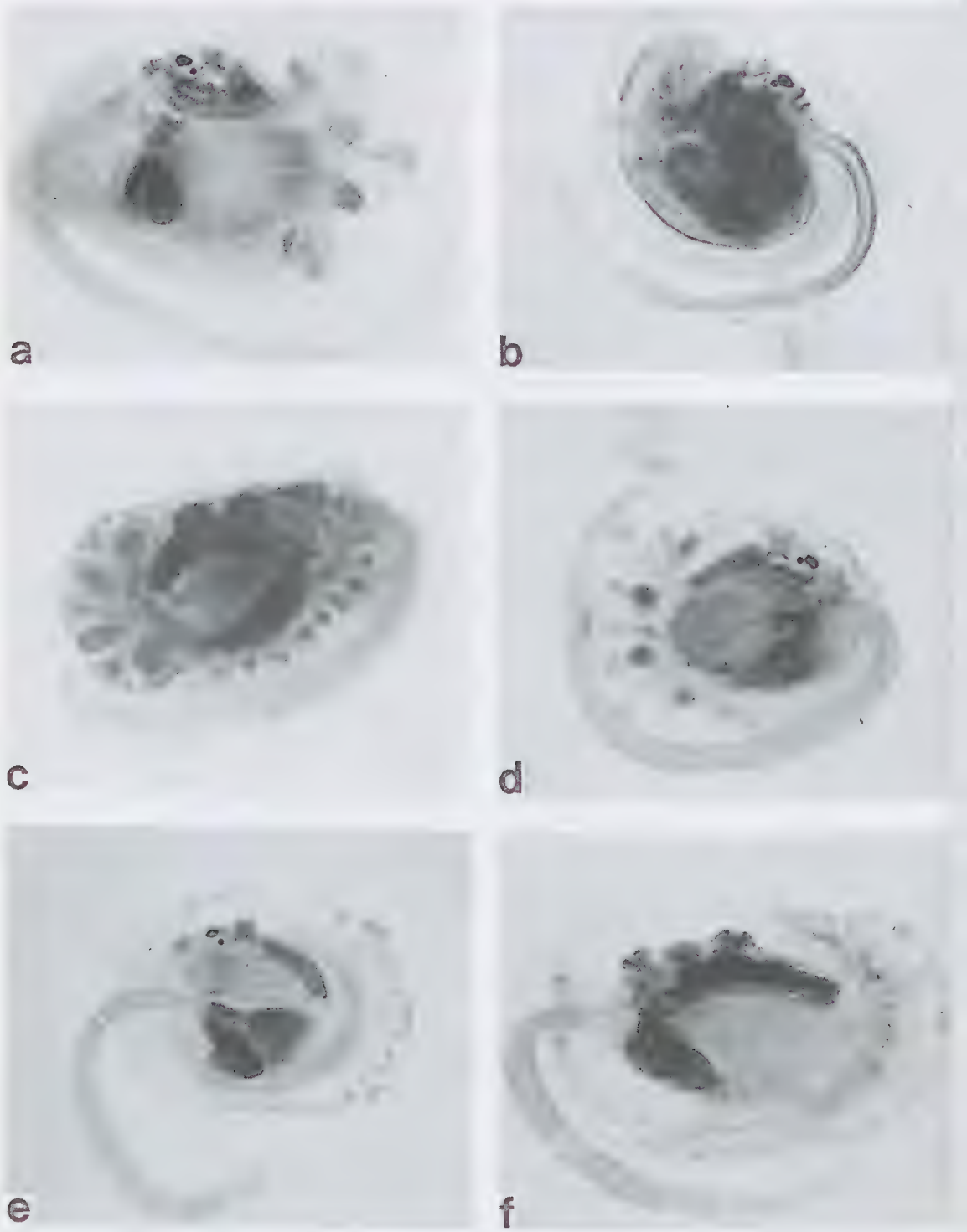
Parallel reduction in the size of zooids often results in convergent evolution, especially in size (number of rows of stigmata and number per row) of the branchial sac and size of larvae. Some taxa (*Pseudodistoma*, *Polyclinum*) have zooids and larvae with conservative morphology, and differences in colonial systems and colony shape and texture often determine species-level taxa. Zooid and larval morphology are more diverse in *Ritterella*, *Synoicum*, *Aplidiopsis* and *Aplidium*, with differences in the atrial aperture, stigmata, stomach wall and arrangement of larval ampullae and vesicles, as well as features of the colony and its systems, providing characters for species determination. Other characters, such as the nature of the larval adhesive apparatus, presence of branchial papillae, length of the oesophagus, nature of the stomach wall, and shape of the posterior abdomen and arrangement of male follicles in it, are significant indicators of relationships at higher (genus or family) taxon levels.

Sixty-two of the total of 110 species treated in this work are new. Many may be indigenous, but these families are not always well sampled, not often being found intertidally. Collection by SCUBA diving enables a diversity of habitats to be sampled and the range of forms treated in this work is largely the result of efforts of these divers. Other difficulties in studying this group, which have resulted in synonymy and misidentification, are colour variation and its post mortem change and loss, loss of colony and zooid turgor obscuring their shape and arrangement, and contractibility of zooids obscuring their morphology.

The most diverse genera in these waters are in the Polyclinidae, in which zooids are organised around well developed cloacal cavities. *Aplidium* is the most diverse genus, and is well represented in both tropical and temperate waters by species with large and conspicuous colonies. Of the families with independently opening zooids without cloacal systems, Pseudodistomidae and Ritterellidae are well represented, especially in certain temperate locations. Euherdmaniidae and Protopolyclinidae are less diverse although each contains some species with wide temperate geographic ranges common in certain locations.

☐ *Indo-West Pacific, Ascidiacea, Aplousobranchia, Placentelidae, Protopolyclinidae, Ritterellidae, Euherdmaniidae, Pseudodistomidae, Polyclinidae.*

Patricia Kott, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia. *1 April, 1992.*



Frontispiece: larvae of Aplousobranchia — **a**, *Pseudodistoma australe* (see Fig. 17g); **b**, *Euherdmania digitata* (see Fig. 13f); **c**, *Polyclinum fungosum* n.sp. (see Fig. 25d); **d**, *Aplidium inflorescens* n.sp. (see Fig. 82c); **e**, *Aplidium altarium* (see Fig. 62e); **f**, *Aplidium filiforme* n.sp. (see Fig. 75e).

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INTRODUCTION

Ascidians of the suborders Phlebobranchia (one of the 2 suborders of the order Enterogona) and Stolidobranchia (the only suborder of the order Pleurogona) were reported on in part 1 of the present work (Kott 1985); and 7 families of Aplousobranchia (the other suborder of the Enterogona) were dealt with in part 2 (Kott 1990). The following account (part 3) continues the review of the Aplousobranchia, dealing with genera formerly contained in the family Polyclinidae Milne Edwards, 1842. These genera are here assigned to 6 different families, 5 of them new (Table 1).

Didemnidae (Aplousobranchia), the only family not yet treated, will comprise part 4 of this monographic treatment of the Ascidiacea in Australia.

The collections on which the work is based are those set out in parts 1 and 2 (Kott 1985, 1990). Museums housing the material examined are referred to by the following abbreviations: AM, Australian Museum, Sydney, New South Wales; BM, British Museum (Natural History), London, UK; QM, Queensland Museum, Brisbane, Queensland; SAM, South Australian Museum, Adelaide, South Australia; TM, Tasmanian Museum, Hobart, Tasmania; MV, Museum of Victoria, Melbourne, Victoria; NTM, Northern Territory Museum, Darwin, Northern Territory; WAM, Western Australian Museum, Perth, Western Australia; USNM, US National Museum of Natural History, Smithsonian Institution, Washington DC, USA; ZMA, Zoological Museum of Amsterdam, Amsterdam, Netherlands; ZMC, Zoological Museum, University of Copenhagen, Copenhagen, Denmark. AMPI refers to the Australian Marine Photographic Index (Neville Coleman).

All specimens referred to by a museum registration number have been examined in the course of the present study. A registration number in italics refers to a sampled portion of the preceding colony.

Throughout this work, the characters of species are summarised to provide a general overview of the diversity of each genus. Dichotomous keys are presented as aids to the identification of taxa at all levels. They have been prepared, as far as possible, to reflect phylogeny. This type of key is generally used for biological material in preference to tabular keys such as those in Monniot (1987). The latter provide too rigid a framework for the analysis of diverse biological material, communicate only a limited amount of information, lack the flexibility to distinguish between convergent and phylogenetic relationships, are open to subjective interpretation, and are unnecessarily unwieldly and ambiguous to use.

Procedures for collection and examination of species are set out in Kott (1990). Examination of specimens is by stereoscopic and compound light microscopy. All larvae are described from stained and mounted specimens taken from adult colonies as indicated.

ACKNOWLEDGEMENTS

I am grateful to those of my collegues, as set out in parts 1 and 2, who, in various material ways, have contributed to the preparation and presentation of these volumes; and to those who have made less tangible, but equally significant contributions by their support and encouragement.

The black and white figures were prepared from camera lucida and other sketches of the specimens by Stephen Cook (Figs 1a–d, 2–6, 7b–d, 8a, 9a–f, 11a–f, 13a–e, 14, 17b–3, 18a–c, 19, 21a, 24, 27, 28a, 35a,b–e); Lucille Crevola Gillespie (Figs. 7a, 17a, 22a); and John Kennedy (all other figures including the larvae of all taxa). Peta Woodgate typed the manuscript. I am grateful to them all. Sue Boyd with Christine Mateira in the Museum of Victoria; Penny Berents in the Australian Museum, Loisette Marsh with Jean Thipthorp in the Western Australian Museum, and Wolfgang Zeidler with Karen Gowlett Holmes in the South Australian Museum have been co-op-

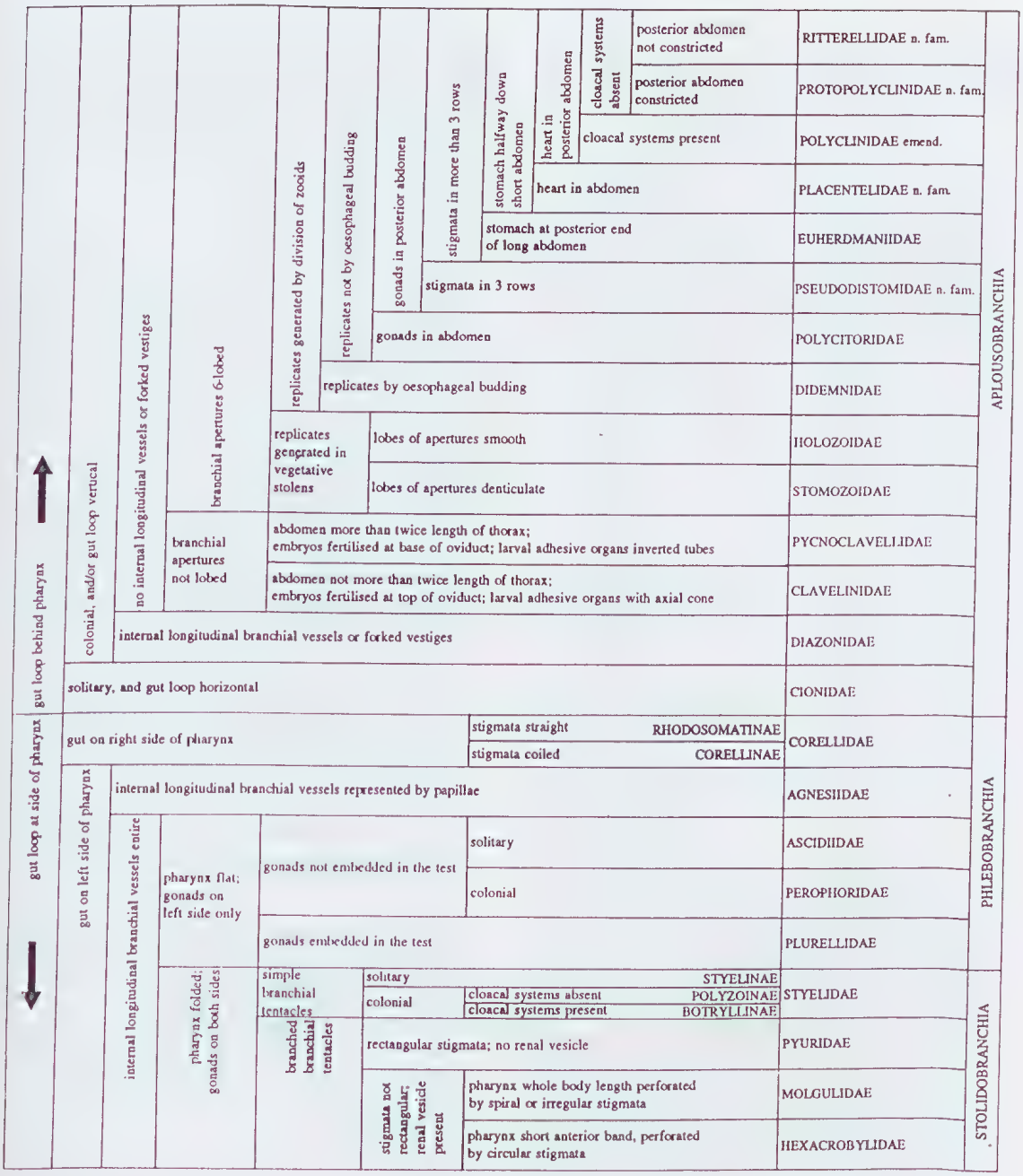

TABLE 1. Ascidiacea – Graphic Key to families

erative and prompt in response to my many requests for large specimen loans.

During 1991 large collections from all around Australia also became available to me from the Australian Institute of Marine Science (AIMS), Townsville, through Dr Peter Murphy. This important collection was made by Rob McCauley and his colleagues (AIMS Bioactivity Group), by SCUBA, as part of their Shallow Water Marine Organism Collection Program for the National Cancer Institute (1992-1996). This collection includes photographs of the living colonies *in situ*. The voucher specimens are now registered in the collection of the Queensland Museum.

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ANNOTATED GLOSSARY

A discussion of the morphology of aplousobranch ascidians and their larvae in the Australian Ascidiacea Part 2 (Kott 1990) refers particularly, although not exclusively, to families reviewed therein. Morphological features, and their variations and functional implications that have not been discussed previously, are reviewed in the glossary that follows. It should be used in conjunction with the glossaries in parts 1 and 2 (Kott 1985, 1990) to appreciate the full range of functional adaptations and other morphological variations in ascidians, (with the exception of the Didemnidae).

adhesive organs: Each of the 4 types of adhesive organs present in the families discussed below, occurs also in other possibly related aplousobranch families.

1. Deeply invaginated tubular adhesive organs, as in Pycnoclavellidae, are in Euherdmaniidae. They are arranged in a triangle when 3, or in the median line when only 2. They suggest a relationship with Pycnoclavellidae.
2. The 3 median adhesive organs in Pseudodistomidae have a hollow, completely eversible axial protrusion in a deep epidermal cup and are either sessile or stalked. The axial protrusion is flat-topped or conical, and apparently lacks the columnar cells found in the axial cones of Holozoidae (*Distaplia*: see Cloney 1977). When everted it is thin-walled and balloon-like, and may have closer affinities with the adhesive organs of Pycnoclavellidae than any others.
3. The 3 median adhesive organs in Protopolyclinidae are stalked, and have an axial cone composed of long columnar cells in a deep epidermal cup. They resemble the adhesive organs of Holozoidae (see Cloney 1977) and Didemnidae (see Turon 1991).
4. The 3 stalked adhesive organs in the anterior mid-line in Ritterellidae and Polyclinidae have a shallow, wide axial cone in a tight epidermal cup. These resemble the adhesive organs of Polycitoridae, although they are smaller. Their relationship to the adhesive organs of Clavelinidae, and Holozoidae awaits investigation.

Epidermal ampullae may also have an accessory adhesive function. (See also **larvae, ampullae, vesicles**).

ampullae, epidermal —, larval —: Outgrowths of the anterior larval epidermis, possibly accessory adhesive organs. In Aplousobranchia they are absent from *Pycnoclavella*, *Euherdmania* and a few other species level taxa in other genera in which size reduction appears to have resulted in simplification.

Ampullae project from the base of triradial adhesive organs (Clavelinidae, Holozoidae). Ampullae arise from lateral ridges along each side of median adhesive organs and also from the median line alternating with them (Polycitoridae, Protopolyclinidae n.fam., Ritterellidae n.fam., Pseudodistomidae n.fam., Polyclinidae). In the new families Protopolyclinidae (*Monniotus*) and Ritterellidae (*Dumus*), and in Polyclinidae (*Polyclinum*, *Aplidiopsis* and some *Aplidium* spp.) the terminal ends of the ampullae have a cap of modified, possibly secretory cells. (See **larvae, vesicles**).

ampullary vesicles: see **vesicles**

anal opening, anus: The rectum continues anteriorly, embedded in the body wall along the dorsal border of the pharynx. Its opening into the atrial cavity is invariably bilabiate in the present aplousobranch families. Its position relative to the atrial apertures (which are normally antero-dorsal) appears determined by selective pressures affecting the position of gonoducal openings. Faecal pellets are found in the rectum but never in the atrial cavity. Presumably, when necessary, the anus is brought into a position near the base of the atrial siphon by muscular action, so that the faecal pellets can be ejected directly to the exterior. Although the oviduct is sometimes diverted into a brood pouch, or is turned ventrally, the opening of the vas deferens is usually associated closely with the anus, the advantage possibly being that sperm also can be expelled directly to the exterior with the excurrent water.

In Placentelidae n.fam., in which numerous embryos are incubated in what probably is an elaborate brood pouch in the distal part of the oviduct (where it lies in the atrial cavity), the anus is in a primitive position in the anterior part of the atrial cavity, opposite the second or third row of stigmata. This is in a position comparable with most Diazonidae, in which the gonoducal openings, at the base of the atrial aperture, are associated with the release of gametes directly to the exterior for external fertilisation.

The anus and gonoducal openings are at mid-thoracic level in most other genera discussed below. In all these families fertilisation and incubation is either in the atrial cavity or in the distal part of the oviduct. Only in Euherdmaniidae and the (probably) related Pycnoclavellidae, both with characteristically long abdomina, are anal and gonoducal openings at the base of the atrial cavity; and in both fertilisation is at the base of the oviduct — at the posterior end of the long abdomen.

apertures: In most aplousobranch ascidians, irrespective of the form of their systems, branchial apertures are 6-lobed. Exceptions in which the branchial apertures are 8-lobed are in some *Ritterella* spp. (viz. *R. pedunculata*), *Aplidium* spp. (e.g. *A. amorphatum*, *A. protectans*) and *Morchellium*. Apparent subdivision of branchial lobes in some species *Aplidium* (e.g. *A. macrolobatum* n.sp. and *A. incubatum* n.sp.) results from contraction of a band of muscles that extends up the centre to the tip of each lobe.

Separately opening 6-lobed atrial, as well as branchial, apertures interrupt the surface test of colonies

in the new families Placentelidae, Protopolyclinidae, Ritterellidae, Euherdmaniidae, and Pseudodistomidae. None of these contain genera with true cloacal systems although other colonial systems, or rudimentary cloacal systems, sometimes occur. Some narrow, stalked Ritterellidae n.fam. (*R. asymmetrica*, *R. pedunculata*) have the zooids in colonial systems with atrial apertures in a row along one side of the flattened, terminal edge of each stalk, and branchial apertures in a row on the opposite side. In other species (*R. papillata* n.sp., *R. cornuta* n.sp., *R. compacta* n.sp.) the atrial apertures are in the centre of the terminal end of lobes of the colony surrounded by the branchial apertures to form rudimentary cloacal systems in which excurrent water from all zooids is ejected in a single stream from the centre of the circular system. Similar rudimentary cloacal systems occur in Polycitoridae (see Kott 1989, 1990). At least in *R. cornuta* n.sp., *in situ* photographs show the flat terminal end of the colony lobe directed away from the oncoming current; and the excurrent stream of water from the centre of each end is entrained by the current as it passes the colony. The arrangement of the apertures of the separate zooids of *Monniotus* spp. is similar to *Ritterella asymmetrica* and *R. pedunculata*, with atrial apertures on the convex side of the spoon-shaped head, and branchial openings on the concave side. A large flap of test along their upper margin directs the branchial apertures downwards (Kott 1989). Also in Protopolyclinidae n.fam., colonial systems of *Condominium* n.gen. have zooids arranged in single lines along flat fan-shaped lamellae. Atrial apertures open in a line on the convex side of the lamella, near and parallel to the top of the colony, on the opposite side to the groove in which the branchial apertures are concealed. The row of atrial apertures are also concealed in a groove when zooids contract.

Very likely the linear arrangement of zooids and their apertures in the hard, sandy, often rigid test is a result of the pressures to direct and separate the respective incurrent and excurrent ciliary streams in these species with separately opening zooids. The compression of the atrial aperture into a transverse opening or slit and the division of its rim into an anterior and a posterior lip usually with 6 lobes on each (e.g. *Monniotus*, *Condominium* gen. nov. and some sandy *Ritterella* spp.) further controls and directs the incurrent and excurrent streams of water.

The relatively large, usually gelatinous, separate zooids in Euherdmaniidae often have large external lobes around the apertures (e.g. *E. dentatosiphonis*, *E. translucida* n.sp.) that resemble those of Stomozoidae (see Kott 1990), although in the latter family the zooids are not separate, being embedded in common test. The function of these enlarged lobes around the apertures, which involve the test as well as the body wall of the zooids, is not established. It is possible that they help to direct the ciliary current, and, to some extent may act as sense organs through the pigment spots at their base which, like similar pigment spots in *Ciona*, Diazonidae and some Phlebobranchia (see Kott 1985, 1990), may be light sensitive. Generally, the lobes around the apertures have musculature associated with the longitudinal muscle bands of the thorax, and the sphincter muscle that surrounds each aperture behind the lobes.

Zooids in stalked colonies of Pseudodistomidae are arranged in the colony like those of some species of Clavelinidae (*Nephtheis*), and Holozoidae (*Sigillina*), all with atrial apertures uppermost and branchial apertures directed toward the stalk so that each stalked head forms a single colonial (but not cloacal) system as discussed by Kott (1989, 1990).

In Polyclinidae, the zooids are arranged in cloacal systems, either around cloacal cavities, or along each side of canals that converge to common cloacal apertures. The atrial apertures open into the sides or base of these cloacal cavities or canals. The openings either are relatively large, exposing part of the branchial sac to the cloacal cavity (as in *Sycozoa* or *Distaplia*); or there is a short, narrow protuberant siphon with a distinct sphincter muscle and a small terminal aperture. Each opening has a flattened atrial lip (or tongue) projecting from its upper rim or from the body wall anterior to the opening. This projection is strap- or leaf-like, triangular or subdivided into 2 or 3, and its tip is straight edged, pointed, bi- or tri-dentate or serrated. Sometimes the circular muscle around the opening continues through the base of the lip, and muscle fibres from the sphincter extend out into the lip (e.g. *Aplidium uteute*, *A. altarium* and the majority of *Synoicum* spp.). Other species, usually with protuberant siphons, have the sphincter muscle (and the aperture) independent of the atrial lip (*Aplidium crateriferum* and related species, and *Polyclinum* spp.).

The size of the atrial lip varies according to its role in effecting the closure of cloacal apertures and contraction of the cloacal canals. An example can be seen in *Polyclinum vasculosum* in which the anteriorly oriented atrial aperture is in the base of the cloacal canals, while the large atrial lip stretches along the top of the canal, and in some cases reaches and is inserted into the test around the cloacal aperture.

ascending limb of gut loop: see **gut, gut loop**.

atrial aperture, — lip, — tongue: see **apertures**.

atrial cavity: In taxa in which it opens directly to the exterior through a 6-lobed atrial aperture, the atrial cavity, its size varying with the size of the thorax, is a relatively contained chamber in which (often large) numbers of embryos complete their development to tailed larvae. Only in some *Pseudodistoma* is a special incubatory pouch constricted off from the atrial cavity.

In Polyclinidae the atrial cavity is a similarly contained chamber in those species in which the atrial aperture is a small anteriorly directed circular opening separate from the atrial tongue (viz. many *Polyclinum*, *Sydneioides*, and *Aplidium* species, and some *Synoicum* species). In the species in which the

atrial tongue is part of the rim of the aperture and the circular muscles of the aperture diverge out into the atrial lip, the aperture itself is less restricted, and when relaxed is a large opening exposing the atrial cavity directly to the cloacal cavity. Both types of atrial aperture are present in *Aplidium* and *Synoicum*. No apparent correlation exists between the size and form of the atrial aperture and cavity and the size and number of embryos being incubated in the chamber. Only in *Polyclinum*, in which small circular atrial apertures prevail, are the embryos and larvae consistently small (trunk appreciably less than 1 mm long). In this genus embryos also are relatively numerous (usually more than 5 being incubated at a time). Although large atrial cavities result from the relatively narrow branchial sacs in the wide thoraces, the embryos seldom fill the atrial cavity, and in many species they are removed entirely from it, being incubated in a brood pouch separate from the atrial cavity. Under these circumstances, the atrial cavity is not occluded by embryos, and possibly remains functional during the period of their development.

The atrial cavities of small *Aplidium* zooids with short, narrow branchial sacs, are relatively small and are subject to further constriction by longitudinal muscles which extend the length of the zooids.

Other variations in the configuration of the atrial cavity occur as a result of the connectives which conduct transverse muscle fibres from the transverse branchial vessels across the atrial cavity to the parietal body wall. In the large zooids of *Synoicum castellatum* n.sp. a row of these connectives appears to divide the atrial cavity into dorsal and ventral chambers (see *S. castellatum* n.sp. below). It is possible that these chambers are present also in smaller zooids, but not so readily observed.

In the taxa reviewed below, the ventral pouches in the atrial cavity observed in *Sycozoa* and *Distaplia* (see Kott 1990) are not present. These are formed where the cavity extends ventrally over the perforated area of pharyngeal wall but does not penetrate over the triangular areas of imperforate pharynx between the ventral ends of the rows of stigmata. (See also **incubation of embryos**).

branchial papillae: possible vestiges of the branchial papillae which support the internal longitudinal branchial vessels in Phlebobranchia, and some aplousobranch families (Cionidae, Diazonidae), occur in Protopolyclinidae n.fam. (*Protopolyclinum*, *Monniotus*), Ritterellidae n.fam. (*Ritterella compacta* n.sp., *R. cornuta* n.sp., *R. multistigmata* n.sp., *R. papillata* n.sp.) and Polyclinidae (*Polyclinum*). These branchial papillae are flat, rounded to short tongue-like projections from the transverse vessels.

Nothing is known of their function and their status as vestiges of phlebobranch branchial papillae is speculative.

branchial sac: In the present group of families the branchial sac becomes progressively smaller, with fewer stigmata and fewer rows of stigmata, in parallel with the reductions in zooid size. Similar trends can be observed in Polycitoridae (*Polycitor* to *Eudistoma*) and Holozoidae (*Sigillina* to *Sycozoa* and *Distaplia*). Placentelidae n.fam. have a large broad pharynx with many rows of numerous stigmata. In Protopolyclinidae n.fam. the number of rows of stigmata as well as the length of each row are as great or greater (up to 20 rows of up to 50 stigmata in *Condominium* n.gen.) than in Placentelidae n.fam. In Ritterellidae n.fam. the zooids are reduced in size and although stigmata are in up to 16 rows, often there are only 5, and in *Dumus* only 4. The number of stigmata in each row are similarly reduced from a maximum of 35 to 12.

The branchial sacs (together with the solitary zooids) of *Euherdmania*, which does not replicate as freely as other taxa, remain relatively large with numerous rows of up to 100 stigmata per row.

Pseudodistomidae n.fam. have 3 long rows of stigmata, in a wide pharynx.

The greatest size reduction in zooids can be observed in the polyclinid genus *Aplidium* in which prolific replication occurs, and zooids are arranged in cloacal systems. In this genus the stigmata occasionally are in only 5 rows. Although the length of the stigmata often is reduced, the number of rows is not, and most species have from 12 to 20 rows of stigmata. *Synoicum* species have similar reductions in size of the branchial sac. The most conspicuous difference between these genera and other polyclinid genera is their reduction in the size of the perforated pharynx. *Polyclinium* and *Aplidiopsis* have relatively large branchial sacs.

Internal longitudinal branchial vessels are present only in Cionidae and Diazonidae; and the only vessels in the branchial sac of all other aplousobranch taxa are transverse. The primary transverse vessels are the unperforated expanses of the pharyngeal wall between the rows of stigmata. On their mesial side, the walls of these vessels are ciliated endoderm projecting into the lumen of the pharynx. On the parietal side the epithelium is ectodermal and not ciliated. Transverse muscle fibres are in the transverse vessels and these join the muscles of the parietal body wall through connectives that cross the atrial cavity (see **atrial cavity**; *Synoicum castellatum* n.sp., below)

Parastigmatic vessels, extending across the stigmata halfway between the primary transverse vessels, sometimes subdivide the stigmata along their length creating additional rows. More often they occur in species with long stigmata and persist as inconspicuous strands which hold the delicate interstigmatal bars in place, and prevent distortion of the stigmata. Parastigmatic vessels occur in Protopolyclinidae n.fam. (*Monniotus* spp. and *Condominium* n.gen.) and Ritterellidae n.fam. (e.g. *Ritterella asymmetrica*, *R. multistigmata* n.sp.). Despite the large size of *Euherdmania* zooids, the stigmata are relatively short and disposed in numerous rows. Parastigmatic vessels are not known in this genus nor are they known in the short branchial sacs of Pseudodis-

tomidae n.fam. In Polyclinidae they are known in some species of *Aplidium* with relatively large branchial sacs (e.g. *Aplidium amorphatum*, *A. parastigmaticum* n.sp.).

branchial tentacles: although these are not specifically counted in the descriptions that follow, a ring of short, relatively stumpy tentacles of various sizes is always present at the base of the branchial siphon, protecting the incurrent aperture. Intrageneric variations in the tentacles do not appear significant taxonomically.

branchial vessels: see **branchial sac**.

brooding, brood pouch: see **incubation**.

budding: see **replication**.

cloacal cavities, — systems: As in Polycitoridae (see Kott 1990) some other taxa with independently opening atrial apertures and embedded zooids have their zooids arranged in incipient or rudimentary cloacal systems. Thus, in Ritterellidae n.fam., *R. papillata* n.sp. and *R. cornuta* n.sp. have zooids arranged in circles with their atrial apertures in a depression in the centre of the circle and their branchial apertures around the periphery; and in *R. compacta* n.sp. the excurrent apertures open into a circular chamber lined with sand which appears to be an invagination in the surface of the colony.

In Polyclinidae a high degree of organisation into cloacal systems is achieved. These systems range from simple circles of zooids around circular chambers with a central cloacal aperture to rows of zooids arranged along each side of branching canals which converge to a cloacal aperture. Sometimes partitions of zooid-free test occur between adjacent systems, or between parts of the same system (i.e. between converging canals); but in other species the systems are crowded together. In preserved or contracted colonies, zooid-free areas of test, being solid and without cloacal cavities or chambers containing zooids, are prominent and usually protrude from the surface. This is an artefact, for in living, extended specimens, the cavities and zooids are expanded and the surface over them is not depressed.

In Polyclinidae there are relatively few taxa (compared with Holozoidae) in which the colony is a single system (e.g. *Aplidium australiense*, *Polyclinum orbitum* n.sp.). More often colonies, even those with large, regular, circular systems are relatively irregular, and contain a number of cloacal systems, each with a conspicuous cloacal aperture. The systems have the capacity to subdivide forming relatively large, bulky colonies. Despite the capacity of Polyclinidae to form large colonies of one or more systems, the cloacal cavities themselves are relatively narrow canals and small, rounded chambers rather than the extensive 3-dimensional cavities of Didemnidae.

The strength and rigidity of the test, especially when this is firm and gelatinous, or contains embedded sand and/or calcareous particles contributes to the maintenance of colony shape including surface features such as ridges and grooves that affect the organisms' interactions with the environment (such as direction of current flow: Kott 1989). The pressure of excurrent water in the common cloacal cavity (when one is present) also contributes to maintenance of the shape and the configuration of the surface, of the colony. Thus, both factors contributing to the strength and rigidity of the test (such as embedded sand), and also to the turgidity of a large, 3-dimensional cloacal cavity (such as efficient replication increasing the number of zooids contributing to the internal pressure within the cloacal cavities), constitute adaptive advantages favoring the evolution of large, 3-dimensional colonies.

In some species of *Polyclinum*, the surface test has a thin, brittle layer of sand but the internal test is soft. In this case their round colony shape may be maintained by the water pressure in the large pharynges of the crowded zooids rather than the brittleness of the surface layer of test. (See also **apertures, colonial systems, colonies**).

colonial systems: In other taxa with independently opening atrial apertures, the zooids are not embedded in common test; or are arranged in colonial systems other than cloacal ones; or, rarely, do not have any obvious systematic arrangement in the colony. *Monniotus* and *Euherdmania* zooids either are solitary; or separate from one another, attached to common test or stolons only at their posterior end, and, like separate Diazonidae, Clavelinidae, and Pycnoclavellidae, function as solitary individuals and do not form systems of any kind. As with cloacal systems, other sorts of systems have zooids so arranged to ensure that the functioning of the whole colony exceeds the efficiency of the sum of its component zooids.

Although zooids of *Ritterella compacta* n.sp. *R. cornuta* n.sp. and *R. papillata* n.sp. are in circular rudimentary cloacal systems with their atrial apertures in the centre, *R. asymmetrica*, *R. pedunculata*, *R. multistigmata* n.sp. and *Condominium* gen. nov. have their zooids arranged around fan-shaped stalked colonies, with the branchial and atrial apertures on opposite sides of the colony margin. Incurrent and excurrent streams, respectively, reinforce one another, and are kept apart; and the long narrow stalks enable the colony to change its orientation with the prevailing currents.

Stalked *Pseudodistoma* with all atrial apertures directed to the top of the colony and the branchial apertures directed downwards towards the point of attachment are equally flexible with regard to changes in current flow. Other benefits from this uniform arrangement of apertures include protection of the open incurrent apertures from falling sediments (Kott 1989; see also **apertures, cloacal systems**).

colonies: The size and form of colonies reflects their phylogeny, toughness of test and amount and type of embedded material. More primitive families such as Diazonidae, Clavelinidae and Pycnoclavellidae, do not usually form particularly large self-supporting colonies. However, generally other aplousobranch

families have firm and gelatinous test, resembling the test of phlebobranch families in consistency; or it is strengthened externally or throughout with sand or other hard (including calcareous) particles. When strengthened, large often complex self-supporting colonies are formed. Occasionally species such as *Pseudodistoma fragile* and *P. gracilum* with particularly soft almost fluid test also have relatively large colonies, possibly occupying sheltered habitats.

The complexity of colonies of the Ascidiacea is most evident in colonies in which the embedded sand makes the test hard, brittle and allows it to form massive 3-dimensional branching colonies (e.g. *A. solidum*); or in intricate colonial systems (e.g. *A. crateriferum*, *Condominum areolatum* n.gen., n.sp.). However, although complexity in shape appears to require sand or other inclusions in the test, the size of colonies *per se* is not related to sand inclusions (e.g. gelatinous colonies of *Polycitor* and *Aplidium* become as large as some of the sand-strengthened colonies in these genera).

As well as affecting the size and form of the colonies, the consistency of the test, which is directly affected by the type and quantity of material embedded in it affects the configuration of the surface test, which, in turn, can modify the currents flowing over the colony and influence its interactions with the environment. In many *Ritterella* spp. and in *Monniotus* a layer of brittle sand-embedded surface test protects the incurrent and excurrent apertures and separates the currents flowing through them. In Polyclinidae the operation of the colony is enhanced by its ability to sort sand and to determine precisely its distribution. For instance, in *Aplidium tabascum* n.sp. a single line of fine sand particles outlines the margins of the firm zooid free areas that protect the branchial apertures; and in *A. caelestis* and *A. macrolobatum* n.sp. fine sand particles are embedded in the thin, flexible test over cloacal cavities, while coarser grains are in the rigid test between the systems.

Colony size and shape does not appear affected by the development of cloacal systems, except that colonies consisting of a single system are a finite size and shape (e.g. *Aplidium altarium* n.sp.) and generally are smaller and more regular than those with multiple systems.

Environmental pressures such as substrate and current flow probably have most influence on the size and shape of the colonies found in any habitat. Thus stalked species appear to occupy habitats where surge alternates the direction of water flow past the zooids; and large spherical, oval, or irregular colonies occupy sea floor habitats at depths where strong currents are not likely to dislodge them from substrates.

Extensive areas of sandy substrate favour large mixed populations of *Monniotus radiatus* n.sp., *Dumus areniferus*, *Ritterella pedunculata*, *R. asymmetrica*, and *R. papillata* n.sp., which all have similar fine, sandy, finger-like colonies embedded in sand — the individuals being more or less held together and stabilised by the sand that accumulates around them (see Kott 1989); and, at the same time, they stabilise the sand. As well as these narrow stalked colonies with hair-like test projections and basal stolons that form sandy aggregates and mats in and over the substrate (e.g. *Pycnoclavella* spp.: Kott 1990, *Ritterella* spp., *Monniotus* spp.), there are other types of colonies that stabilise sandy substrates and protect them from erosion. These are colonies with basal test forming root-like projections that hold them firmly in the substrate (e.g. *Aplidium geminatum* n.sp.), and colonies embedded in the substrate and forming 3-dimensional reticula and branching lamellae (e.g. *Aplidium acroporum* n.sp., *A. petrosum* n.sp., *A. solidum*, and *Polyclinum terranum* n.sp.). (See also **cloacal cavities, colonial systems**).

descending limb (of gut loop): see **gut.**

dorsal lamina, — languets: No continuous fold occurs along the mid-dorsal line of the pharynx in Aplousobranchia as in some Stolidobranchia and Phlebobranchia. Instead pointed languets arise from the transverse vessels to the left of the mid-line, and curve over to the right. These channel the mucous food cord (gathered from the sheets moving dorsally over each side of the pharynx) as it moves posteriorly to the oesophagus.

duodenum: see **gut.**

epidermal ampullae: see **ampullae.**

epidermal vesicles: see **vesicles.**

excurrent aperture: see **apertures.**

fertilisation: About half the extant Ascidiacea are solitary species which, with few exceptions (see below), are externally fertilised. The other half are colonial, and these, with the exception of the Diazonidae, are fertilised internally. The colonial species are predominantly Aplousobranchia, although taxa of Phlebobranchia (Perophoridae) and Stolidobranchia (Botryllinae and Polyzoinae) are included. Solitary species are predominantly Stolidobranchia and Phlebobranchia, only 2 genera of Aplousobranchia (*Ciona* and *Rhopalaea*) being included.

With the exception of *Polycarpa* and some Molgulidae and Agnesiidae, solitary Ascidiacea have long and relatively few male and female gonads, and their ducts open together near the anus, at the base of the atrial siphon. Released gametes thus are ejected, and presumably dispersed with the excurrent ciliary stream. Gametes also are released in the excurrent water as the animal rythmically squirts to irrigate the atrial and branchial cavities. In both cases waste products and gametes are projected well away from the animal where they are not likely to contaminate the incurrent stream (see Hoshino *et al.* 1986, Kott 1989b).

If both male and female gametes of the same mature individual are released together there would be opportunities for self-fertilisation. However there is growing evidence that individuals are generally self-sterile (Santis and Pinto 1991, Fuke 1983, Kawamura *et al.* 1987, Cloney 1990, Litscher and

Honegger 1991). Further, species are not necessarily functional hermaphrodites, and may be either protandrous or protogynous. Other mechanisms may exist to prevent self-fertilisation, one being the possibility that ejected sperm are dispersed further away than ova.

The stimulus for release of gametes is not understood, although their are obvious advantages for one to exist. Under certain conditions light is known to trigger gamete release. Carlisle (1951) proposed that *Ciona intestinalis* released gametes and stopped secreting mucus from the endostyle in response to the presence of a gamete of the same species in the incurrent feeding stream. Although it is an apparent advantage for mucus secretion to stop when fertilisation is internal, it is not for externally fertilised species.

In *Polycarpa*, short gonads and their ducts are scattered over the body wall, and the openings of the ducts are removed from the atrial aperture. Presumably this results in longer retention of gametes of both sexes in the atrial cavity than would be the case if they were released at the base of the atrial siphon. In certain species (*P. intonata*, *P. tinctor*, *P. tinctorella*: see Kott 1985) even longer retention results from the ventral orientation of the short gonoducts, and indeed these species are internally fertilised and embryos are brooded in the atrial cavity. Certain molgulid species are analgous to *Polycarpa* in respect to the arrangement of their male and female gonoducts, and also are internally fertilised, brooding, species. They all have the oviducal apertures turned ventrally, and the openings of the vas deferens distant from the atrial aperture. *Molgula calvata* and *M. manhattensis* (see Kott 1985) have short, multiple openings of the sperm duct along the length of the ovary; and *M. ellistoni*, *M. sabulosa* and *Eugyra* spp. (see Kott 1985) have a short vas deferens, at the proximal end of the ovary, turned ventrally. Although the reproductive strategy of *Adagnesia* spp. is not known, both gonoducts are turned ventrally (see Kott 1985) and probably embryos are brooded internally. Only one species of the Pyuridae, *Pyura littoralis* (see Kott 1985), has short female ducts while retaining a long vas deferens. This may be an adaptation for internal fertilisation, although embryos have not yet been found in the atrial cavity.

It is not known if these internally fertilised solitary species are self-sterile or not. If they are, the reasons for the adaptations found in the majority of these species, which apparently ensure the retention of sperm as well as ova in the atrial cavity, are difficult to understand. Further, if they are self-sterile, it is possible that mucus secretion is interrupted to allow sperm for cross fertilisation to reach the atrial cavity through the pharynx. In *Ecteinascidia turbinata*, at least, it appears not to be drawn in through the atrial aperture with relaxation of body muscles following contraction and squirting (Ryland *pers. comm.*).

Whereas only relatively few solitary species have evolved devices for internal fertilisation, this strategy is universal in colonial species, and once it has evolved it appears never to be lost. The family Diazonidae, which contains some genera retaining a solitary habit, and the related and supposedly primitive solitary Cionidae are the only aplousobranch taxa externally fertilised.

In colonial internally fertilised species (as in solitary ones) the position of each gonoduct relative to the others and to the atrial aperture probably is related to patterns of gamete release and fertlisation. Although the oviduct is often displaced when it acts as a brood pouch, the vas deferens and anus of colonial species open together, usually part of the way up the thorax, and not necessarily close to the atrial aperture. The atrial cavity, although it is often distended with embryos, never contains faeces outside the rectum, and presumably faecal pellets are released by the contraction of the body wall muscles, which irrigates the atrial cavity and brings the anus close to the atrial aperture. Since the opening of the vas deferens is associated with the anus it is possible that gametes are also released in this way. In holozoid genera with cloacal systems, and in the Didemnidae, large atrial apertures often expose anal and gonoducal openings directly to the cloacal cavity. This also happens in some Polyclinidae (*Aplidium*, *Synoicum* and a few *Polyclinum*). Thus, the opening of the male duct of colonial, internally fertilised species (as in solitary externally fertilised ones) is usually positioned where sperm released from it are most likely to be expelled to the exterior, either directly or through the cloacal cavity, rather than being retained in the atrial cavity for self-fertilisation. It is not known whether or not embedded colonial zooids have a pattern of rythmic squirting, like solitary and independent colonial ones, to increase means by which sperm might be released.

Further, colonial, like solitary, species have been shown to be self-sterile (e.g. *Diplosoma listerianum*: Ryland and Bishop 1990; *Botryllus schlosseri*: Sabbadin 1979). In addition to the growing evidence of cytological and chemical mechanisms for self-sterility, the existence of functionally gonochoric colonies in the genus *Syzozoa* (see Kott 1990), and of sequentially hermaphroditic colonies in many other taxa, support the view that colonial, as well as solitary, ascidians are not generally self-fertilised. Sabbadin (1979) reports a protogynous condition for *Botryllus*. Further evidence of protandry or protogyny exists when embryos but not mature male gonads are present and when there are mature male gonads but no embryos suggesting that the male gonads mature either before or after the female ones (see below).

If, as the evidence suggests, internally fertilised colonial species are not self-fertilised, sufficient concentrations of sperm must reach the atrial cavity from outside the zooid for some to enter the oviduct, and move to the fertilisation chamber (the brood pouch, or the proximal end or top of the oviduct, or the atrial cavity) at the time that oocytes reach maturity. Thus it is probable that advantages associated with the

synchronous release of gametes are as great in internally fertilised colonial species as they are in externally fertilised solitary ones, especially as colonial zooids are small, with relatively small ovaries, few ova and often ephemeral gonads. Again, little is known of mechanisms triggering such a synchronous release. Further it is not known how sperm enters the atrial cavity. Ryland (*pers. comm.*) found that external material was not drawn into the atrial cavity of *Ecteinascidia turbinata* following its partial evacuation by squirting. It is not kown whether or not embedded zooids do squirt, however even if they do it seems unlikely that sperm could enter zooids through common cloacal chambers against the direction of the ciliary current. Even in independently opening zooids it is unlikely that it would enter directly through the atrial aperture. The alternative hypothesis is that the process reported by Carlisle (1951) for *Ciona intestinalis* is present in colonial species viz. that mucus secretion is interrupted so that sperm entering the pharynx can pass through the stigmata into the atrial cavity, thence into the oviduct

The only colonial, internally fertilised families which seem to be analogous with *Polycarpa*, *Molgula*, *Eugyra* and *Adagnesia* species (with short, and ventrally directed vas deferens suggesting retention of sperm in the atrial cavity) are Pycnoclavellidae and Euherdmaniidae, with the gonoducal and anal openings at the base of the atrial cavity. Possibly these families also have mechanisms to prevent self-fertilisation.

The relatively large size of the testis in relation to the ovaries in most colonial species indirectly supports the view that generally cross- rather than self-fertilisation is likely. Otherwise the production of a large amount of sperm for the fertilisation of few oocytes within the same zooid in colonial species would not be economic. Further, it is difficult to entertain an hypothesis that the well established mechanisms ensuring self-sterility reported in Cionidae (see Kawamura *et al.* 1987, Cloney 1990, de Santis and Pinto 1991), Ascidiidae (Litscher and Honegger 1991) and Pyuridae (Fuke 1983) are exceptions from a general condition; especially when selection for short-lived free-swimming, viviparous larvae occurring simultaneously (see Kott 1974, 1982) results in the maintenance of crowded populations with maximal opportunities for gene exchange. (See also **incubation of embryos**).

gastric folds: see **gut**.

gastro-intestinal gland: see **gut**.

gonads: unlike the families discussed in Part 2 (Kott 1990) in which they are in the gut loop, the testis follicles and small ovary of most of the families discussed below are in a posterior abdomen behind the gut loop. The exceptions are some *Euherdmania* (*E. digitata*, *E. dentatosiphonis*, *E. translucida* n.sp.) in which they sometimes are in the gut loop, and *Sidneioides* in which the ovary is in the thorax. In Protopolyclinidae n.fam., *Polyclinum* and *Aplidiopsis* the testis follicles are bunched together in a sac-like posterior abdomen separated from the abdomen by a narrow neck with the small ovary surrounded by the testis follicles. In *Sidneioides* a similar sac-like posterior abdomen contains the male follicles, but the ovary is halfway up the thorax, with a short oviduct opening directly into the atrial cavity.

In other taxa (*Euherdmania*, *Ritterella*, *Aplidium*, *Synoicum*, *Morchellium*) there is no constriction between abdomen and posterior abdomen. The testis follicles in these taxa either are bunched together in a short, thick posterior abdomen, or arranged in one or two longitudinal series in a sometimes thread-like posterior abdomen which is many times the length of the rest of the zooid. In many species of Pseudodistomidae n.fam. gonads seem intermediate between those with testis follicles bunched behind the ovary, and those with testis follicles in a longitudinal series in the posterior abdomen. In most known species of this family the male follicles are bunched together around the ovary in a small part of a long thread-like posterior abdomen. In specimens of *Pseudodistoma candens* n.sp., the vas deferens, distended with sperm, is seen to originate at a point level with the ovary, about halfway down the cluster of male follicles, as if the gonads had turned onto their side to fit into the thin posterior abdomen. *Pseudodistoma gracilum* n.sp. and *Synoicum atopogaster* have a similar arrangement of male follicles.

In genera with male follicles in longitudinal series the ovary is invariably anterior to them and the vas deferens is joined by short vasa efferentia as it extends up the side of the posterior abdomen. When 2 series of testis follicles are present the vasa efferentia alternate between the rows. Male follicles are in a single series when a second is not developed. This appears to be an ephemeral condition and does not constitute a genetic difference. Male follicles arranged in longitudinal series can appear bunched when they are drawn together with contraction of the long posterior abdomina. However, in certain species (*Aplidium altarium*, *Aplidium uteute*) the testis follicles are actually bunched, with short vasa efferentia joining them to a relatively short vas deferens, in a short posterior abdomen.

The ovary is always small in these families, producing relatively few eggs for internal fertilisation and brooding. Testes, however, are relatively large, but always composed of numerous separate follicles rather than a large single one, as in most taxa of the Ascidiacea. Large, undivided testes are present only in some *Perophora* spp., and in some Polyzoinae (see Kott 1985; see also **fertilisation**).

gonoducal openings, gonoducts: see **fertlisation**.

gut, gut loop: Distal to the large pharynx, the gut of aplousobranch ascidians always forms a simple, narrow and usually vertical U-shaped loop, which occupies the length of the abdomen. In the present group of families (characterised by the presence of the gonads behind the gut loop in a posterior abdomen), the range of variations resembles those found in those aplousobranch families in which the gonads

are enclosed in the gut loop (see Kott 1990). These variations are:

1. The length of the oesophagus. In Euherdmaniidae this is long, as it is in Pycnoclavellidae and Polycitoridae and to some extent in Clavelinidae, with the stomach in the posterior end of a long abdomen. The oesophagus is relatively short, with the stomach halfway down the abdomen, in Protopolyclinidae n.fam., Ritterellidae n.fam. and Polyclinidae (as it is in Holozoidae and some Clavelinidae). In Pseudodistomidae n.fam. (as in Diazonidae) the oesophagus is of various lengths, sometimes being moderately long. It is almost twice the length of the post-pyloric part of the gut loop in *Pseudodistoma aureum* and even longer in *Anadistoma* n.gen. Occasionally a prestomach enlargement is in the oesophagus, as in *Aplidium altarium*. The only other genus in which this is known is *Clavelina* (*C. moluccensis*, *C. cylindrica*: Kott 1990).

2. The orientation of the stomach. This usually is oblique to the long axis of the zooid, with the oesophagus curving ventrally to enter the cardiac end of an asymmetrical stomach with a short dorsal border and a long curved ventral border. Only in *Aplidium*, *Morchellium*, and in some species of *Ritterella* is the oesophagus straight, entering the cardiac end of a more or less radially symmetrical, vertical barrel-shaped stomach.

   In *Polyclinum* and *Sidneioides* the gut loop usually is horizontal, and slightly twisted, the right or descending limb moving around to lie above the ascending limb, and the posterior end of the loop curving dorsally. The horizontal orientation of the gut loop is reminiscent of Cionidae, and Holozoidae (*Sycozoa*, *Distaplia*).

3. Post-pyloric subdivisions of the gut. These consist of a wide duodenum immediately behind the stomach, and a narrow mid-intestine that expands into a large oval, posterior stomach about halfway along its length. There is thus a proximal (post-pyloric) part of the mid-intestine, as well as a distal (pre-rectal part). This arrangment is found in most other aplousobranch families (see Kott 1990). Only very rarely is there a departure from this pattern — viz. in Pseudodistomidae n.fam. the proximal part of the mid-intestine is wider than usual and is more or less continuous with the duodenum, an external crease marking their junction.

   Pockets in the proximal end of the rectum on each side of its junction with the distal section of the mid-intestine form a rectal valve in many species of aplousobranch, especially *Ritterella*, *Aplidium*, *Aplidiopsis*, *Synoicum*, *Polyclinum*.

   It is possible there are some intraspecific variations in the development of this valve and its appearance is affected by artefacts of preservation and gut contents. It is associated with the long, straight, vertical ascending limb of the gut loop in these families of the Aplousobranchia.

4. The stomach wall is either smooth, both inside and out, interrupted only by a typhlosole (or suture line) along the dorsal border; or it is folded; or, as in *Synoicum*, *Morchellium* and *Aplidiopsis*, its internal lining is raised into circular or irregular glandular areas, and the external surface may also be raised into mulberry-like swellings.

   In *Pseudodistoma* the short, wide stomach is partially divided into 4 shallow, longitudinal compartments. *Aplidium* species, with relatively small zooids and narrow short stomachs, have a relatively large glandular area achieved by longitudinal folding of the stomach wall into from 5 to 30 often deep folds. *Euherdmania*, *Monniotus* and *Ritterella* have similar, though not so numerous longitudinal folds in the stomach wall.

5. A gastro-intestinal gland, with a duct from the pyloric end of the stomach breaking into branches around the ascending limb of the gut, probably always is present in all families of Aplousobranchia, although it is usually conspicuous only in Polycitoridae, and has a storage vesicle only in some Holozoidae.

head: The expanded terminal free end of stalked solitary and colonial ascidians is termed the head. It accommodates the thoraces, which, when expanded, are the widest part of the zooid or individual, and colony and zooid openings are on its surface. The narrow abdomina and posterior abdomina are in the stalk.

heart: The heart is a delicate curved tube in the posterior end of the posterior abdomen in most of the genera discussed below. The exception is *Placentela*, the monotypic genus from the north-western Pacific, which has its heart in the abdomen, presumably retained there in a primitive position while the gonads spill back behind the gut loop (see Nishikawa 1984b).

incubation of embryos: all families discussed in the present work are internally fertilised and embryos, brooded internally by the parental zooids, are released as tailed larvae. The process of replication is well developed. Zooids as a consequence are small and simplified, but numerous (see Kott 1990). Thus, despite the fact that in most cases the embryos are relatively small (< 1 mm) and yolky, few are produced and incubated at a time by any one zooid. The number of larvae being produced by the whole colony is maintained by the large numbers of zooids producing few embryos, rather than few zooids producing a large number.

Larger embryos are found in *Euherdmania*. In this genus eggs are fertilised at the base of the oviduct and are incubated in the oviduct as they move up the long abdomen, as in the possibly related Pycnoclavellidae (see Kott 1990). Relatively large embryos are also produced in *Pseudodistoma* in which the eggs of some species appear to be fertilised and incubated, usually one at a time, in a brood pouch constricted off from the posterodorsal corner of the thorax.

In most of the other taxa discussed below, eggs are fertilised, and the relatively small embryos are incubated in the atrial cavity. Only in *Polyclinum*, which has zooids with large roomy atrial cavities, do the

Ampullae	Adhesive organs (type)	Adhesive organs (arrangement): Triradial — No vesicles	Median linear — No vesicles	Median linear — With vesicles (except in some simplified Polyclinidae): Vesicles separate from paired postero-ventral, dorsal, and sometimes anterior epidermal strands	Median linear — With vesicles (except in some simplified Polyclinidae): Vesicles separate from paired ventral and dorsal epidermal strands	Median linear — With vesicles (except in some simplified Polyclinidae): Vesicles separate directly from epidermis along lateral, and sometimes, median lines
No ampullae	Thin-walled everting tubes	Pycnoclavellidae *Sigillina mjöbergi* Euherdmaniidae				
With ampullae (except some simplified Polyclinidae)	Thin-walled everting cylinders or spheres		Pseudodistomidae			
	Axial cones or platforms large: wider than deep	Clavelinidae	*Sigillina* *Hypodistoma* *Eudistoma* *Polycitorella*			
	Axial cones moderate to large: deeper than wide	Holozoidae (except: *Sigillina*, *Hypodistoma*)	*Polycitor* *Cystodytes*	Protopolyclinidae		
	Axial cones small: wider than deep			Ritterellidae (not aequalisiphonis group) *Polyclinum* *Synoicum* spp.	*Synoicum* spp. *Aplidium lunacratum* *Aplidium multilineatum* *Aplidium ornatum* *Aplidium protectans* *Aplidium robustum* *Aplidium tabascum*	*Ritterella* spp. (? aequalisiphonis group) *Synoicum* spp. *Aplidium* spp.

TABLE 2. Summary of epidermal elements at anterior end of larval trunk in aplousobranch families.

particularly small embryos (larval trunk seldom more than 0.6 mm long) appear not to occlude the pharynx, even when relatively large numbers are present at a time (up to 12 embryos: *P. fungosum*). Nevertheless, it is in this genus that a brood pouch sometimes is present (*P. marsupiale*, *P. tsutsuii*, *P. terranum* n.sp.) constricted off from the body wall in a unique position, about halfway along the dorsum of the thorax at the level of the anus. It is most probable that fertilisation as well as incubation of embryos, takes place in it; or in the atrial cavity.

Only very few *Aplidium* species (*A. uteute*, *A. altarium*) have a brood pouch, at the postero-dorsal corner of the atrial cavity, in which embryos are incubated. In this genus, fertilisation generally appears to be in the top of the oviduct or in the atrial cavity.

incurrent aperture: see **apertures**.

larvae: The larvae of the taxa formerly grouped in the single family Polyclinidae, as originally defined, demonstrate its polyphyletic nature. The larvae of the new families proposed below can be characterised by their size, adhesive organs, ectodermal vesicles and ectodermal ampullae (see Table 2). The Euherdmaniidae have adhesive organs that are invaginated tubes that evaginate on settlement, as in the family Pycnoclavellidae; the relatively large larvae of Pseudodistomidae n.fam., as do Polycitoridae, have large adhesive organs and ectodermal ampullae be-

tween and lateral to the median adhesive organs; the generally smaller larvae of Polyclinidae *emend.*, Protopolyclinidae n.fam., and Ritterellidae n.fam. usually have ectodermal vesicles which separate off from the larval epidermis into the test between and alongside the median adhesive organs. There are also differences between genera in the origin of the ectodermal vesicles (see **vesicles** below).

All the larvae of the families discussed below have a discrete mass of yolk cells in the middle of the trunk. Larval ocellus and otolith are present in all genera. Although *Euherdmania* has similar adhesive organs to *Pycnoclavella*, the larvae do not appear to have a tendency to loss of the ocellus as do those of *Pycnoclavella*.

With the exception only of *Euherdmania* in which the invaginated tubes are triradially arranged, the 3 adhesive organs are in the anterior median line. Only *Aplidium triggsense* (with 12), and *A. multipapillatum* Millar, 1975 (with 8), have a different number of adhesive organs, all in the median line.

muscles: With the exception of sphincter muscles around the apertures, the body musculature in the parietal body wall is usually longitudinal, although fibres are exchanged with adjacent bundles. Transverse fibres are present, forming a network with the longitudinal ones, only in *Ritterella multistigmata* n.sp. and *Anadistoma* n.gen. These transverse fibres may originate as branches from the longitudinal muscle bands. Also in *Ritterella*, oblique muscles similar to those in the Clavelinidae cross the thorax from the endostyle to the postero-dorsal corner of the thorax. Longitudinal and oblique muscles extend in a band along each side of the abdomen and posterior abdomen, as they do in most of the genera. Only some *Aplidiopsis* species, *Polyclinum* and *Sidneioides* are exceptions with short longitudinal muscles confined to the anterior part of the thorax.

In some Pseudodistomidae n.fam. (*P. oriens* n.sp., *P. candens* n.sp) at least some fibres of the longitudinal muscles extend along a vascular stolon posterior to the posterior abdomen and heart. The presence of these muscles on the long, distinct vascular stolon is reminiscent of *Sigillina* (Holozoidae, see Kott 1990). The presence of both a gonad-containing posterior abdomen, and a vascular stolon with muscles (apparently homologous with a similar organ in *Sigillina*) in certain *Pseudodistoma* species suggests that the vascular stolon of Holozoidae is a separate structure rather than being homologous with the posterior abdomen of Polyclinidae, Ritterellidae n.fam., Pseudodistomidae n.fam. and Protopolyclinidae n.fam.

In all taxa, transverse fibres are present in the transverse vessels. These are fibres that derive from longitudinal muscle bands. These muscles are seen clearly in the large zooids of *Synoicum castellatum* n.sp., branching off longitudinal muscles and entering the transverse vessels through connectives from the parietal body wall about one-third of their length from the dorsal mid-line. Ventrally they divide into branches each side of the endostyle.

The large atrial lips of *Polyclinum* and species of other genera in Polyclinidae are also muscular. Branches from the ventral thoracic longitudinal muscles extend out into these tongues, and circular muscles from around the atrial apertures also are diverted out along them. These large atrial lips insert into the test to protect the atrial openings into the cloacal cavities, and in some cases, insert into the rim of common cloacal apertures and exert some control over these excurrent openings.

Anteriorly, the longitudinal muscle bands extend onto the siphons, where there is exchange of fibres with circular (including sphincter) muscles, longitudinal fibres are then organised into bands, one extending into the each lobe around the rim of the aperture. When these muscles are concentrated into the tip of each lobe they depress it and divide the tip of the lobe into 2 (e.g. *Ritterella dispar*, *Aplidium macrolobatum* n.sp.).

parastigmatic vessels: see **branchial sac**.

posterior abdomen: see **gonads**.

replication: In these well developed aplousobranch families replication takes place by horizontal division of the posterior abdomen and/or the abdomen, and usually is prolific. The process has not been specifically studied in Australian species. However the process is similar in the range of polyclinid species studied by Berrill (see 1935 for review), Nakauchi (1966–1987), and Nakauchi and Kawamura (1974a–1986). The process is the same in *Ritterella* (see Nakauchi 1977).

Generally reserve food cells (trophocytes) pack the abdomen and posterior abdomen. Sometimes the thorax and abdominal organs are resorbed but in other species they remain functional during the budding process (see *Ritterella pulchra*: Nakauchi, 1977). The abdomen and/or posterior abdomen are then divided, by constriction of the epidermis, into numerous buds. A segment of epicardial tube is contained in each, and is the regenerative tissue for the new vegetative zooid which develops from each bud.

In *Polyclinum* vegetative zooids with relatively long strap-like vegetative posterior abdomina (as opposed to the short sac-like posterior abdomen of sexual zooids) are found crowded in the growing margins of colonies (see *P. vasculosum*).

Although moderately long, sometimes branched, vascular appendices are present in Ritterellidae, and shorter ones are present in most of the other families, these seem not to be involved in the process of replication as they are in Holozoidae.

Pseudodistomidae n.fam. have a long vascular stolon with longitudinal body muscles extending along it as in *Sigillina* (Holozoidae). This supports the view that this family is related to *Sigillina* (Holozoidae). The method of replication in the Pseudodistomidae n.fam. is not known, nor is it known that the vascular appendix has a role in the process. Although Brewin (1958) found 'bud-like masses' lying be-

neath the zooids of *P. cereum*, and juvenile replicate zooids are found in the stalk of developing lobes of *P. oriens* n.sp., it is not known whether these developed from the vascular stolon in a process that resembles that of Holozoidae (see Kott 1990); or if they developed from the posterior abdomen and/or abdomen of the parental zooids by horizontal strobilation, as in Polyclinidae. A continuation of the epicardial tube into the vascular stolon of *Pseudodistoma* has not been found.

stomach: see **gut**.

test: see **cloacal systems, colonial systems, colonies**.

trophocytes: see **replication**.

vascular appendix, — process, — stolon: see **replication**.

vesicles, ampullary —, epidermal —, larval —: Hollow spheres, about 0.01 to 0.05mm diameter with an epithelial wall, usually occur in the test of the larval trunk in Protopolyclinidae, Ritterellidae and Polyclinidae. The fine strands attaching them to the larval epidermis sometimes sever as larvae mature. Like the enlarged epithelial cells on the tips of some ampullae, the epidermal cells occasionally are larger on the outside surface of the vesicle than on its mesial wall.

In *Monniotus* (Protopolyclinidae), *Polyclinum* and *Synoicum*, the vesicles exclusively branch off fine strands that detach from the epithelial wall on each side of the mid-line and trail through the test. The ventral strands arise from about one half to two-thirds of the way from the anterior end of the trunk, one extending to the posterior end of the trunk near the posterior-horns of the haemocoelic cavity where the vesicles form a tight cluster, and another shorter one trails anteriorly. Similar pairs of epithelial strands from the anterior end of the dorsal surface trail posteriorly on each side of the dorsal mid-line to the vicinity of the branchial aperture, and in *Monniotus* a corresponding pair of strands extend antero-ventrally on each side of the adhesive organs. The vesicles are especially numerous postero-ventrally. Dorsal and ventral clusters of vesicles arising from similar test strands are present in some larvae of *Aplidium* (*A. lunacratum* nom. nov., *A. multilineatum* n.sp., *A. ornatum* n.sp., *A. protectans* n.sp., *A. robustum* n.sp. and *A. tabascum* n.sp.), but the postero-ventral test strand is much shorter and a postero-ventral cluster of vesicles near the base of the tail does not occur. Larvae of the majority of *Aplidium* species have vesicles directly attached by their short sometimes branched hair-like filament to the larval epidermis rather than to an epithelial strand trailing through the test. These vesicles are arranged in single or multiple series to form a lateral arc around the anterior end of the larval trunk on each side of the lateral line, and sometimes also in the median line between the adhesive organs (Table 2).

The enlarged epithelial cells on the outside of the vesicles suggest that they may be involved with adhesion to the substrate.

Vesicles are not present in the larvae of Clavelinidae, Holozoidae, Polycitoridae, Pycnoclavellidae, Euherdmaniidae and Pseudodistomidae n.fam.

Family POLYCLINIDAE *sensu* Milne Edwards, 1842

Polyclinidae Milne Edwards, 1842 is distinguished from other aplousobranch families by the presence of gonads and heart in a posterior abdomen which also serves as the vegetative stolon. Genera of Diazonidae, in which gonads and heart are sometimes in a posterior abdomen, have internal longitudinal branchial vessels to distinguish them. Certain species of Holozoidae have gonads in a posterior abdominal sac but it is separate from the vegetative stolon (see Kott 1990), the holozoid heart is in the abdomen (rather than the posterior abdomen), and the larvae usually have adhesive organs triradially arranged (rather than in the median line). Certain species of *Euherdmania*, formerly assigned to Polyclinidae, have no posterior abdomen and, with the gonads and heart in the abdomen, can be mistaken for *Polycitor*. Larval characters must then be relied on to distinguish them (see below, Euherdmaniidae).

Like Polycitoridae, the present group of families have longitudinal and oblique muscle bands that extend from the thorax along the length of the zooid. Also, transverse muscle fibres are in the transverse branchial vessels. However, usually they lack the thoracic bands that form an external coat in the parietal body wall of Polycitoridae. Exceptions, in which transverse muscle bands are present in the parietal body wall to form a meshwork with the longitudinal ones, are *Condominium* n.gen., *Ritterella multistigmata* n.sp., *Anadistoma* n.gen. and *Euherdmania fasciculata* Monniot, 1983.

Taxa in Polyclinidae were assigned to one of 2 subfamilies, Euherdmaniinae and Polyclininae, grouped on the basis of shared convergent characters. Thus, *Protopolyclinum*, *Euherdmania*, *Dumus*, *Ritterella*, *Placentela*, *Pseudodistoma*, *Monniotus*, *Citorclinum* and their synonyms which lack cloacal systems comprised Euherdmaniinae; and *Polyclinum*, *Aplidium*, *Synoicum*, *Sidnyum*, *Aplidiopsis* and *Morchellium* which all have cloacal systems were in Polyclininae. However, considerations of larval and adult morphology (set out below) suggest other family groupings (Tables 1,2) that more closely reflect their probable phylogeny, and acknowledge closer relationships with other taxa of Aplousobranchia than those with genera formerly included in the polyphyletic Polyclinidae as defined by Milne Edwards (1842) and subsequent authors (see Berrill 1950).

In developing this new classification, the characters that have been relied on to indicate higher taxon relationships include the length of the oesophagus — a short oesophagus one- to two-thirds the length of the abdomen as in Holozoidae, or a long oesophagus more than two-thirds of the length of the abdomen as in Polycitoridae; the presence or absence of structural folds in the stomach wall, and the shape and orientation of the stomach — whether it is vertical and barrel-shaped or oblique and shortened dorsally; the size of the branchial sac, and number of rows of stigmata; the type of larval adhesive organs — eversible axial cones in shallow epidermal cups, or pycnoclavellid inverted, tubular ones; and the site of fertilisation and incubation of embryos, e.g. in the distal (thoracic) part of the oviduct as in Diazonidae (see Protopolyclinidae n.fam., Ritterellidae n.fam.), or in the base (abdominal part) of the oviduct as in Pycnoclavellidae (see Pseudodistomidae n.fam. and Euherdmaniidae), or in the atrial cavity (see Polyclinidae). Generally, the presence of branchial papillae, long and numerous rows of stigmata, the anus opening well anteriorly, a large number of embryos, and bunched male follicles indicate more primitive taxa than those without branchial papillae, and with narrow thoraces, few rows of stigmata, and testis follicles in longitudinal series.

Most of the taxa in these families have well developed rectal caeca (a rectal valve) at the base of the ascending limb of the gut loop. This probably is an apomorphic character associated with the vertical gut loop. It is known also in *Hypsistozoa*, *Neodistoma* and in some *Distaplia* (see Kott 1990).

Of the following 6 families (which include all the genera formerly included in Polyclinidae), only the monotypic family Placentelidae n.fam. from the north-western Pacific does not occur in Australia. In the other families, all reported from Australia, the only genera that do not occur here are *Protopolyclinum* Millar, 1960 (Protopolyclinidae n.fam.), *Citorclinum* Monniot and Millar, 1988 (Pseudodistomidae n.fam.), and *Pharyngodictyon* Herdman, 1886 (Ritterellidae n.fam.).

Key to families of the genera formerly comprising Polyclinidae Milne Edwards, 1842

1. Atrial apertures 6-lobed; cloacal systems rudimentary or lacking 2

   Atrial apertures not 6-lobed; cloacal systems well developed .... POLYCLINIDAE *emend.*

2. Stigmata in 3 rows ..... PSEUDODISTOMIDAE n.fam.

   Stigmata in > 3 rows 3

3. Stomach at posterior end of long abdomen ..... EUHERDMANIIDAE

   Stomach near the middle of short abdomen . 4

4. Heart in the abdomen ..... PLACENTELIDAE n.fam.

   Heart in the posterior abdomen 5

5. Posterior abdomen short, tapering, sometimes separated from abdomen by a constriction ..... PROTOPOLYCLINIDAE n.fam.

   Posterior abdomen not short, tapering, never a constriction between posterior abdomen and abdomen ..... RITTERELLIDAE n.fam.

Family PLACENTELIDAE n.fam.

The monotypic family is characterised by its numerous rows (12 or more) of numerous stigmata (up to 50), relatively short oesophagus, smooth stomach, the anus at the top of the branchial sac (level with the second or third row of stigmata), heart in the abdomen, numerous embryos being incubated in the terminal part of the oviduct in the atrial cavity, almost sessile median larval adhesive organs with an eversible axial cone in an epidermal cup, and 4 rows of stigmata in the larvae. The body muscles are longitudinal and oblique on the thorax and have not been observed on the abdomen or the posterior abdomen.

The type species of the genus *Placentela*, *P. crystallina* Redikorzev, 1913, has been well studied (Tokioka 1968, Nishikawa 1984b). In the latter study Nishikawa examined the existing material (including types) of *Placentela crystallina* and its synonym *Sigillinaria clavata*. The species has embedded zooids and up to 60 eggs and developing embryos in what appears to be an internal brood pouch in the distal end of the oviduct in the atrial cavity. The heart is in the abdomen with the anterior part of the gonads, while the remainder of the gonads and the epicardial sacs are in the posterior abdomen. Gonads spill over from the gut loop into the posterior abdominal extension as they do in *Hypsistozoa* (see Kott 1990). There is parenchymous material in the posterior abdomen of *P. crystallina*, which

Nishikawa (1984b) believed would be the site for formation of replicate zooids.

Kott (1963) first proposed the synonymy of *Sigillinaria clavata* Oka, 1933 and *Homoeodistoma michaelseni* Redikorzev, 1927 with *Placentela crystallina*. All 3 are from the sea of Okhotsk and the Kamchatka Peninsula (north-western Pacific). Nishikawa (1984b) subsequently established the synonymy of *S. clavata* with *P. crystallina*, but did not include *H. michaelseni* in his study. The latter species as well as having the same general colony and zooid morphology (including 12 rows of stigmata, and the anus and gonopores opening at the top of the branchial sac), is sympatric with *P. crystallina* and is here considered synonymous with it.

Species assigned to *Sigillinaria*: Brewin, 1950b (see also Brewin 1958) are not congeneric with *Sigillinaria* Oka (*Placentela*). They have long or short oesophagus, folded or smooth stomach, 3 or more rows of stigmata and some have parastigmatic vessels. Subsequently Brewin (1958) on the basis of "parallelism in classification", reassigned species to genera solely on the presence or absence of stomach folds — those with stomach folds to the genus *Pseudodistoma*, and those without to *Homoeodistoma*. Thus *S. arenosa* Brewin, 1950 and *S. novaezelandiae* Brewin, 1950 were erroneously assigned to *Homoeodistoma* (respectively *Ritterella* and *Pseudodistoma*, see below).

Homoeodistoma longigona Tokioka, 1959 from the Sea of Japan (Wakasa Bay) differs from *H. michaelseni* (*Placentela crystallina*) in the position of the anus (opposite the sixth or seventh row of stigmata — in a pharynx with 20 rows), the position of the heart (at the end of the posterior abdomen), yellow pigment spots in the lobes of the apertures, and a long, narrow posterior abdomen with testis follicles and eggs in longitudinal series. Although a similar longitudinal series of ova is in the proximal end of the oviduct in *Euherdmania*, the long oesophagus of the latter genus is lacking. Millar's (1963) proposal that *H. longigona* is a diazonid may be correct (see Kott 1990, p.33); or it may be related to Ritterellidae (see *R. arenosa* below).

Holozoidae and *Placentela* (see Nishikawa 1984b) have similar large larvae with well developed adult organs and almost sessile adhesive organs, zooids with short oesophagus, and gonads sometimes extending into the posterior abdomen which also contains an epicardial sac. However, in view of the primitive characters of *Placentela*, viz. numerous stigmata, the large number of embryos being brooded, the large testis and the anterior position of the anus, a diazonid ancestor is more likely than a direct relationship.

Although sessile everting adhesive organs and fertilisation at the top of the oviduct occur in Clavelinidae they probably are characters convergent, rather than homologous, with those in *Placentela*. A relationship with Polycitoridae is unlikely in view of the large number of embryos, the relatively short oesophageal neck (the cardiac end of the stomach is about halfway down the abdomen), the anterior position of the anus, and the absence of transverse thoracic muscles.

The type species *P. crystallina*, and *P. translucida* Kott, 1969 from the Antarctic Peninsula are the only species known. The genus has not been recorded from Australian waters. *Placentela areolata* Kott, 1963, *P. ellistoni* Kott, 1972b and *Homoeodistoma omasum* Monniot, 1987 are incorrectly assigned (see *Condominium* n.gen, Protopolyclinidae n.fam. below).

Family PROTOPOLYCLINIDAE n.fam.

Zooids are embedded or separate, with both apertures 6-lobed, the atrial apertures opening separately to the exterior. The pharynx is large, and stigmata are numerous, arranged in 9 or more rows, with or without parastigmatic vessels. Branchial papillae often are on the transverse vessels. The anus opens one third to halfway up the atrial cavity. The oesophagus is short, and curves ventrally to enter the dorsally shortened, obliquely oriented stomach about halfway down the relatively small abdomen. The stomach has (sometimes only faint) longitudinal ridges in *Monniotus*, but irregular ridges or a smooth stomach in the other genera. Gonads, in a broad tapering posterior abdomen (constricted off from the abdomen only in *Protopolyclinum*), consist of numerous bunched testis follicles and a smaller ovary anterior to the testis. Embryos are incubated in the distal end of the oviduct in the posterior part of the atrial cavity.

In the characteristically large thorax, short oesophagus, small abdomen, anterior position of the anus, tapering posterior abdomen, numerous bunched male follicles, and incubation of embryos in the distal part of the oviduct this family resembles *Placentela* (Placentelidae, see above), which, however, differs in having the heart in the abdomen. Further, the presence of branchial papillae, suggests an origin direct from a diazonid ancestor.

The numerous small bunched testis follicles in a broad posterior abdomen, the occasional presence of branchial papillae, the dorsally shortened stomach, and the larval vesicles branching off posteriorly- and anteriorly-trailing stalks on each side of the dorsal and ventral mid-lines suggest a relationship with *Polyclinum*, although *Monniotus*, with shallow longitudinal stomach ridges, may have diverged from the main polyclinid line.

The Antarctic *Tylobranchion* Herdman 1886, has branchial papillae, short oesophagus and folded stomach, but its branchial papillae are forked and it has cionid-type larvae indicating a closer affinity with Diazonidae (see Kott 1990).

Ritterellidae n.fam., often with branchial papillae and larvae like the present family, are distinguished by their narrow zooids, usually with testis follicles in one or 2 longitudinal series and vertical barrel-shaped stomach.

The family, known only from Indo-West Pacific and Australian temperate waters, contains 3 genera, *viz. Condominium* n.gen., *Monniotus* Millar, 1988 and *Protopolyclinum* Millar, 1960 (monotypic, known only from New Zealand).

Key to genera of Protopolyclinidae

1. Zooids embedded 2
   Zooids not embedded ..... *Monniotus*
2. Branchial papillae present; colonial systems not present ..... *Protopolyclinum*
   Branchial papillae not present; colonial system present ..... *Condominium* n.gen.

Genus **Monniotus** Millar, 1988

Type species: *Monniotus ramosus* Millar, 1988

Zooids are contained separately in the terminal branches of the narrow sandy stalks that comprise the colony. The test consists of a delicate membrane to which sand adheres making a firm brittle casing for the zooid which, when expanded, completely occupies the space inside and adheres closely to the inside of the sandy casing. Body muscles are longitudinal, extending the whole length of the zooid. Rows of stigmata are numerous (up to 10) and one or more branchial papillae are on the transverse vessels, and also on the parastigmatic vessels when these are present. The gut loop is short, and the stomach has only very faint internal longitudinal ridges on the parietal wall. The posterior abdomen is long with the small ovary in front of the bunched follicles of the large testis. The posterior abdomen is especially broad when testis follicles are mature. Testis follicles and embryos are never present at the same time, and the genus appears protandrous (see also Millar 1988). Fertilisation is in the distal part of the oviduct (in the thorax), where a longitudinal developmental series of up to 6 embryos at a time are found being incubated. The larval adhesive apparatus resembles that of *Polyclinum*, in the 3 median adhesive organs, epidermal vesicles branching off trailing epidermal strands, and median and lateral ampullae with columnar epithelial cells, similar to those in the adhesive organs, forming a cap on the tip as in *Polyclinum*. However, the adhesive organs themselves are deeper than those in the latter genus.

In all known species, the incurrent aperture opens in the centre of a transverse, curved strip of delicate, sand-free, test. The sand-strengthened test anterior to the naked strip curves down over the aperture to form a protective lip.

Although a phylogenetic relationship is not implied, the colonies resemble those of *Ritterella* spp., especially those of *R. cornuta* which have narrow sandy lobes, regularly spaced branchial papillae and numerous rows of stigmata. However, in *Ritterella* the zooids are organised into single colonial (not usually cloacal) systems, while in *Monniotus* they are separate from one another, one in each lobe of the colony, the lobes joined basally to common stolons. Colonies also resemble those of *Euherdmania claviformis*, having separate zooids in narrow, sandy stalks. Millar (1988) distinguished *Monniotus* from *Euherdmania* by its branchial papillae. However, these are variable, reduced to one per row in *M. australis*. A more reliable and plesiomorphic difference from *Euherdmania* is the short oesophagus, resembling *Ritterella* and *Aplidium* rather than *Pycnoclavella* (to which *Euherdmania* appears to be most closely related).

The genus is recorded only from Australian temperate waters and from the western Indian Ocean. Two of the 3 known species are indigenous to Australian waters. The western Indian Ocean *M. ramosus* most resembles the eastern Australian species *M. radiatus* n.sp., having numerous papillae on each transverse vessel (see below). *Monniotus australis*, known from western and southern Australian waters, has only a single papilla on each vessel — in the centre of each side of the body.

Monniotus australis (Kott, 1957)
(Fig. 1. Plate 1a)

Euherdmania australis Kott, 1957, p. 103 (part, not specimens from Camden Haven *M. radiatus* n.sp.); 1972b, p. 172.

Distribution

New Records: Western Australia (Houtmans Abrolhos, WAM 1016.83; off Dongara, WAM 926.89 929.89). South Australia (Great Australian Bight, SAM E2099–100 E2103 E2416, QM GH4147).

Previously Recorded: South Australia (Elliston Bay — QM G9291 Kott 1972b; Waldegrave I. — SAM E2111–2; Investigator Strait — Kott 1972b). Victoria (Port Phillip Heads — holotype AM Y1317 Y1165 Kott 1957).

Description

External Appearance: The colonies are straight-sided, club-shaped lobes, tapering to common stolons at their narrow basal end. The terminal, expanded part is triangular in section with a flattened, triangular, slightly oblique free end. The lobes are from 1cm (Western Australia and Bass Strait) to 4cm (Great Australian Bight) long, and only rarely divided along their length. Sand grains are packed in a single layer in the very thin test to form a hard, rigid but brittle coat. Delicate internal test without sand is present only posterior to the thorax, which, when expanded, fills the inside of each lobe, the body wall adhering closely to the rigid sand-filled coat. The branchial aperture is directed downwards from the middle of the base of the triangular free end of the head just below its margin. The atrial aperture is directed upwards from just inside the apex of the triangle on the free end of the lobe. The openings are sometimes transverse, with 3 well separated small pointed lobes on each lip of the opening.

Internal Structure: The body wall is very delicate with about 12 fine longitudinal and oblique muscles extending the whole length of the zooid from the thorax to the posterior end of the long, narrow posterior abdomen. About 30 pointed tentacles of various sizes are in a circle around the base of the branchial aperture. The neural duct is short and funnel-shaped with a circular opening into the pharynx. There are 9 or 10 rows of about 30 stigmata anteriorly, but posterior rows are shorter. All except the posterior 3 rows are crossed by a parastigmatic vessel. The transverse and parastigmatic vessels each have a single tongue-shaped to pointed papilla in the centre. Triangular dorsal languets are also on the parastigmatic vessels as well as on the primary transverse vessels. The oesophagus is curved and narrow, opening into the stomach about halfway down the very small abdomen (never more than half the length of the thorax and often less). The stomach has about 12 shallow, often inconspicuous glandular ridges, on its parietal wall. These are obscured when the abdomen is contracted. The mesial wall of the stomach has irregular ridges. A long narrow duodenal region and oval posterior stomach are in the descending limb of the gut loop. A rectal valve is at the junction of the mid-intestine and rectum. The anus opens half-way up the thorax. Its rim is bilabiate, but each lip is subdivided into a fringe of pointed lobes. Gonads consist of numerous small follicles bunched in a long grape-like or narrow cylindrical mass around the vas deferens. A 4- or 5-egg ovary is in the top of the posterior abdomen.

Specimens from Price I. collected in April (QM GH4147), and Encounter Bay collected in October (SAM E2111–2 E2416) have up to 8 embryos aligned in a developmental sequence in the distal part of the oviduct (in the posterior half of the thorax). Thus there appear to be at least 2 breeding seasons.

The larval trunk is 1.1mm long. A median ampulla with a cap of modified columnar epidermal cells is in each interspace between the adhesive organs and 4 rounded lateral ones are on each side of the median adhesive organs. Numerous, crowded ectodermal vesicles are present along each side of the median line from the postero-ventral corner and around the anterior end of the trunk to the branchial aperture. These branch off the sides of fine stalks from the larval ectoderm which trail anteriorly and posteriorly along each side the dorsal and ventral mid-lines of the trunk, and especially cluster around the postero-ventral horns of the haemocoele near the base of the tail. The adhesive organs have an eversible axial cone in a deep tulip-shaped cup.

Remarks

The larval trunk appears to be similar to that of *M. ramosus* Millar, 1988. The branchial sac of the present species (which has a geographical range from western, across southern Australia to Bass Strait) has only a single papilla on each transverse vessel, while the eastern Australian *M. radiatus* n.sp., although it has colonies similar to the present species, has a branchial sac with numerous papillae like that of the African *M. ramosus*.

The zooids appear to arise from a central axial stalk in 2 (WAM 926.89 and 989.89) of the west-

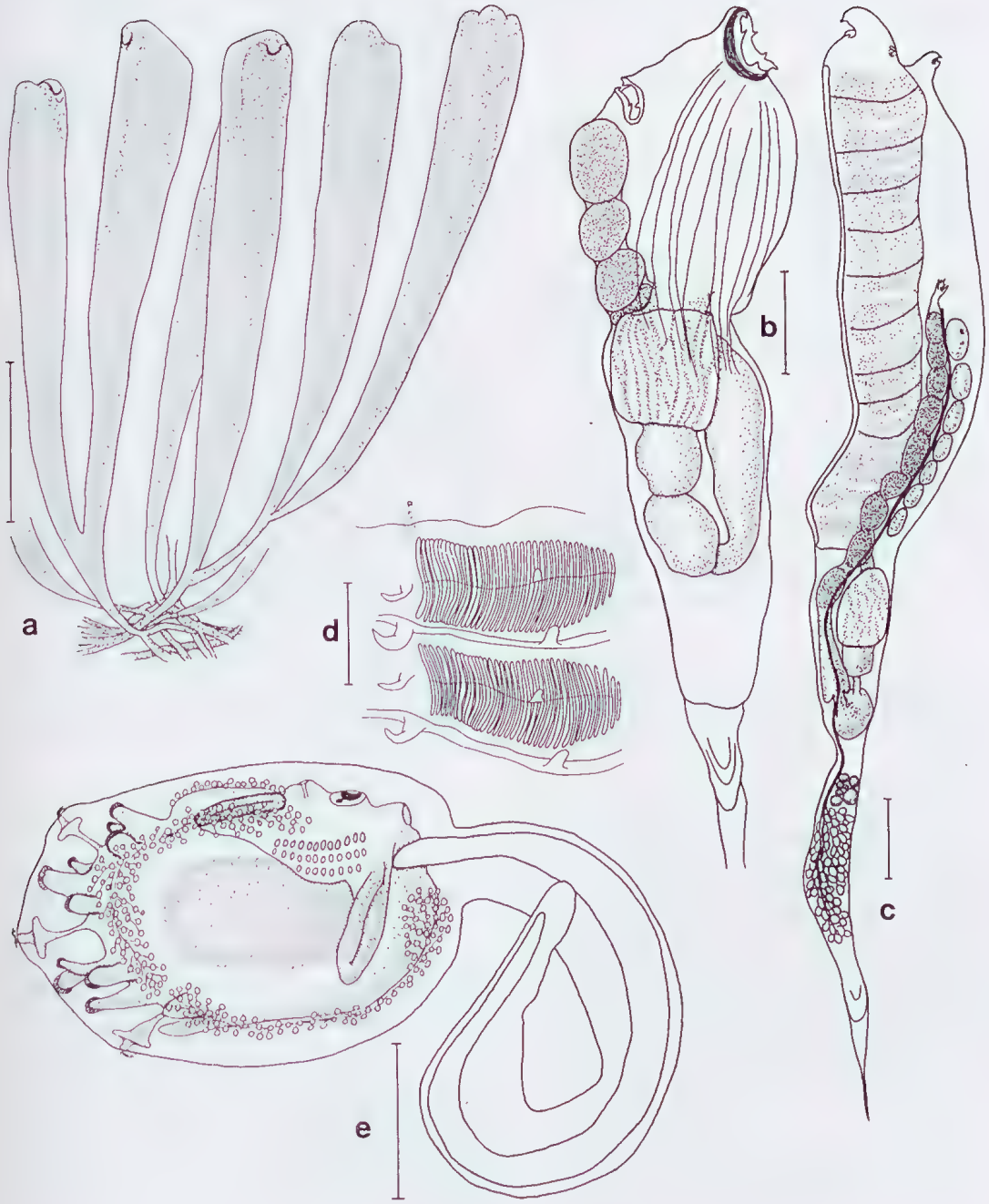


FIG. 1: *Monniotus australis* — **a**, part of colony (QM GH4147); **b**, immature zooid with thorax contracted (WAM 929.89); **c**, mature zooid with embryos in oviduct (SAM E2112); **d**, portion of branchial sac showing papillae on primary transverse and parastigmatic vessels (QM G9291); **e**, larva with some partly everted adhesive organs (SAM E2112). Scales: **a**, 1cm; **b** 0.5mm; **c**, 2mm; **d**, 1mm; **e**, 0.4mm.

ern Australian colonies. However this is only apparent, as zooids radiate out from basal stolons fixed around a stem of weed.

Monniotus radiatus n.sp.
(Fig. 2)

Euherdmania australis Kott, 1957, p. 103 (part, specimen from Camden Haven).

DISTRIBUTION

TYPE LOCALITY: New South Wales (Nambucca Heads, 13m, coll. J.E. Watson 11.1.72, holotype QM G10012 *MV F58435*).

FURTHER RECORDS: Victoria (Portland, QM GH93), New South Wales (Camden Haven — paratypes AM G1356 Y1120 Kott 1957).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are a sandy mass of upright, club-shaped lobes, up to 2.5cm long, often with one or two branches along their length. The widest part, i.e. the terminal free end not more than 3mm in diameter. These lobes arise from a common basal mass. Each lobe contains a single zooid.

The thick, terminal part of each lobe is triangular in section and the free end is a flat isosceles triangle, with the branchial aperture directed downwards from the middle of the base of the triangle, just below its margin. The atrial aperture is directed upwards from the upper surface just inside the apex of the triangle.

INTERNAL STRUCTURE: The contracted zooids are about 8mm long, divided into thorax, short abdomen, and a relatively long posterior abdomen (up to half the total zooid length). Apertures are both 6-lobed on short siphons, the branchial one turned ventrally, and the short, atrial siphon directed dorsally, at right angles to the longitudinal axis of the body. A mesh of very fine longitudinal and transverse muscle bands is on each side of the thorax, and the longitudinal bands continue along each side of the abdomen and posterior abdomen.

The thoraces of these zooids are relatively large, with 9 rows of about 20 stigmata. Each row except the last 3 (in which the stigmata are shorter) are crossed by parastigmatic vessels. Each of the parastigmatic and the primary transverse vessels have about 10 rounded tongue-like papillae on them. The papillae on the parastigmatic vessels are smaller than those on the primary transverse vessels. A pointed trianglar dorsal languet is in the mid-line (over the dorsal sinus) also on both parastigmatic and transverse vessels. The parastigmatic vessels appear to be bisecting the rows of stigmata, and increasing their number.

The oesophagus is relatively short, the small stomach (with 12 shallow longitudinal ridges) is halfway down the abdomen and there is a duodenal region and a mid-intestine in the distal part of the descending limb of the gut loop.

Gonads consist of bunched male follicles and a small ovary. Larvae are not known for this species.

REMARKS

The shape of both colony and zooids, including the orientation of their apertures resemble both the Australian *M. australis* and the type species from Mozambique (Millar 1988). The African species differs from the present one in having less regular colony lobes which branch more along their length and appear to be less rigid, zooids with more rows of stigmata, and without parastigmatic vessels. However, in the present species absence of these vessels from the posterior rows of short stigmata indicates that they are actively bisecting the rows of stigmata to increase their number and this may not be a reliable distinction between the species.

Monniotus radiatus overlaps the range of *M. australis* in Bass Strait.

Genus **Condominium** n. gen.

Type species: *Placentela areolata* Kott, 1963.

The genus has large, embedded zooids, arranged in an integrated colonial system but not in cloacal systems. Six-lobed branchial openings directly to the exterior are on one side of the colony, atrial openings on the other. Stigmata are in numerous (at least 12) rows. Transverse as well as longitudinal muscles are present on the thorax. Parastigmatic vessels are present occasionally, but branchial papillae are not. The oesophagus is short, and curves to open along the dorsal side of the shield shaped, bilaterally symmetrical, smooth stomach which is halfway down the abdomen. Testis follicles are bunched, and the ovary is anterior to the testis.

The genus is monotypic, being known only from its type, an indigenous Australian species with a range around the continent.

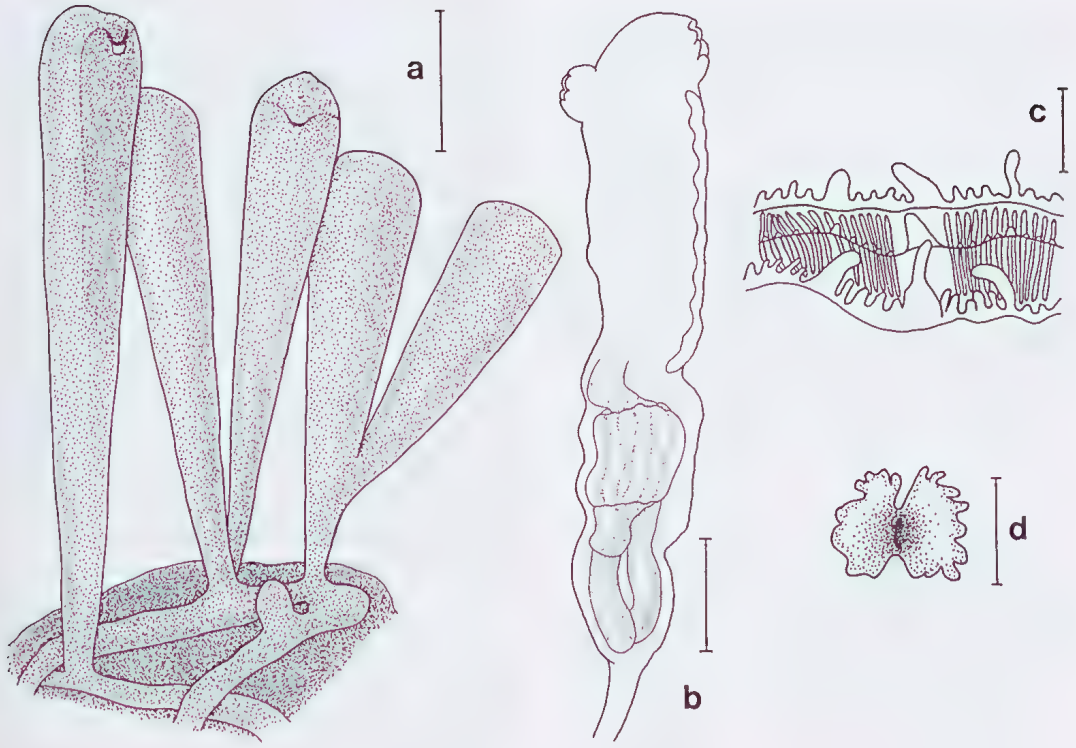


FIG. 2: *Monniotus radiatus* n.sp. (paratype AM G1356) — **a**, part of colony; **b**, zooid; **c**, part of branchial sac showing papillae and dorsal languets on transverse and parastigmatic vessels; **d**, anus. Scales: **a**, **b**, 5mm; **c**, **d**, 0.25mm.

Condominium areolatum (Kott, 1963)
(Fig. 3, Plate 1b–d)

Placentela areolata Kott, 1963, p. 74.
Placentela ellistoni Kott, 1972b, p. 173.
Homoeodistoma omasum Monniot, 1987, p. 503.

DISTRIBUTION

NEW RECORDS: Western Australia (Cockburn Sound, WAM 582.31). South Australia (Taylor I., QM GH4161). New South Wales (Lord Howe Is, QM GH4380). Queensland (Heron I., QM GH4937; Central Section, Great Barrier Reef, QM GH5418). Northern Australia (Torres Strait, QM GH4931–6).

PREVIOUSLY RECORDED: South Australia (Great Australian Bight — AM U3925 Y1316 Kott 1972b). Queensland (Mackay — Kott 1963). New Caledonia (Monniot 1987).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are very irregular, with curved, fan-shaped lamellae, from 2 to 4cm along their outer edges, joined basally to common test, and sometimes forming a cornet. Some specimens have lamellae fitting around one another like the petals of a rose (QM GH4161), but in others they arise at random from the common test. The test is brittle with sand externally, but not internally. Internally only a thin layer of fairly tough, translucent test separates the zooids, which lie parallel to one another in a single layer in each lamella. The branchial apertures, directed downwards, open into a groove that is just behind and parallel to the rounded rim on the outer curve of each lamella. The atrial apertures open horizontally into a less well defined groove on the opposite side (inner curve) of the lamella, lower down than the row of branchial apertures. The grooves receiving the apertures are conspicuous in the preserved specimens, although the sand adhering to the outside of the colony obscures the actual openings. In photographs the atrial apertures of living specimens are seen directed upwards from a convex surface, the groove concealing them having disappeared.

INTERNAL STRUCTURE: Zooids are large but

transparent. Their total length, even when contracted is about 1.5cm, with thorax, abdomen and posterior abdomen of about equal length. The branchial aperture usually is turned ventrally. The atrial aperture extends laterally from about one third of the distance down the dorsal surface (level with the fourth row of stigmata). Each aperture has 6 minute pointed lobes. Numerous parallel longitudinal muscles are on the thorax, and these cross bands of transverse fibres on the parietal body wall outside each transverse branchial vessel. Fibres from these transverse bands continue into the branchial vessels through the branchial connectives. Longitudinal muscles continue along the abdomen and posterior abdomen. There is a strong but narrow sphincter muscle around the base of each short siphon. The opening of the neural gland is a funnel-shaped ciliated pit. The long rectangular stigmata are numerous, about 50 in each of 17 to 20 rows. Branchial papillae are not present. Very fine parastigmatic vessels are present in the colony from Lord Howe I. (QM GH4380), but not in other specimens.

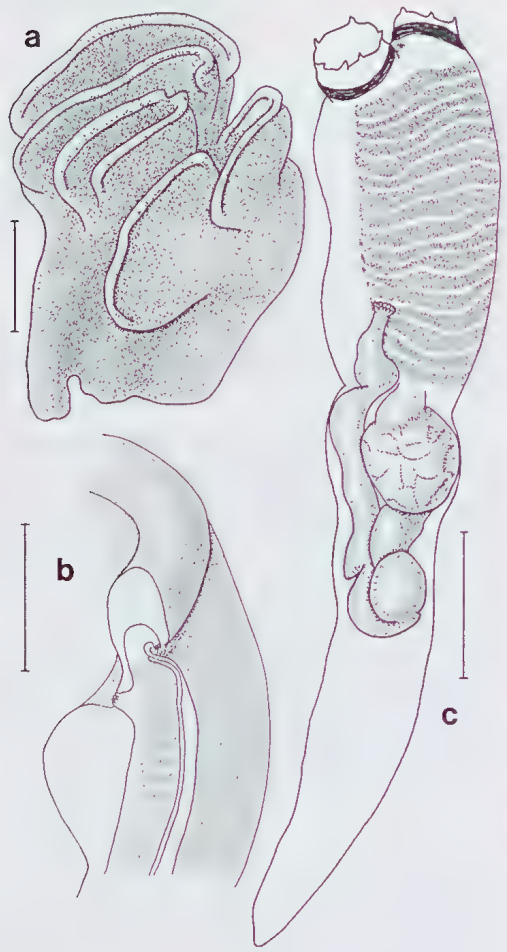


FIG. 3: *Condominium areolatum* gen. nov. — **a**, **b**, colony (QM GH4161) (**a**, external appearance; **b**, section through a lamella); **c**, zooid (QM GH4380). Scales: **a**, 2cm; **b**, 5mm; **c**, 2mm.

The oesophagus is short, and the smooth, almost spherical stomach is in the upper half of the abdomen. The internal wall of the stomach is papillated and sometimes divided randomly into irregular areas and some transverse and irregular wrinkles. Duodenum, posterior stomach and mid-intestine are in the descending limb of the gut loop, the mid-intestine opening into the rectum at the base of the descending or ascending limbs or in the pole of the gut loop. The rectum has two caeca (forming a rectal valve) at its proximal end. The anal opening is near the posterior end of the branchial sac.

Gonads are not present in any of the newly recorded material, although they are present in material from South Australia (Kott 1972b). They consist of a small ovary anterior to the numerous small bunched testis follicles.

Advanced embryos with tails almost completely encircling the trunk (0.44mm) are present in the type material (AM Y3925 Y1316) an ocellus and an otolith are present, but no other organs are developed.

Remarks

Kott (1963) overlooked the unusual and characteristic lamellae in the irregular type colony of *P. areolata* (*Condominium areolatum*).

The colonies of this species (like *Ritterella asymmetrica* n.sp.) have well developed colonial systems that differ from those of most other species of *Ritterella*, which have rudimentary cloacal systems or homologues of them, in which excurrent streams are expelled into depressions or concavities where they reinforce one another (see *Ritterella cornuta* n.sp., below). Instead branchial and atrial apertures, respectively, are in rows parallel with the outer edge, and on opposite sides of the terminal border of colony lobes. In all lobes, the branchial apertures are turned down toward the base of the colony, while the atrial apertures are directed away from it as they are in the separate zooids of *Monniotus*, *Dumus* and *Euherdmania*. In the present species (as in *R. asymmetrica*) the excurrent streams from each of the zooids are separated from incurrent water, and

probably are entrained by the currents that flow over the colony (see Kott 1989).

Colonies newly recorded from Torres Strait are not well preserved. They are very like the more irregular ones of this species taken from other locations, but although the zooids appear to have been identical in size and general outline, details of their structure are obscure.

Homoeodistoma omasum Monniot, 1987 from New Caledonia is conspecific with the present species, its characters falling within the intraspecific range of variations recorded in the Australian populations. Its occurrence in New Caledonia is not inconsistent with the temperate-tropical range recorded for the species.

Despite their considerable colony size and wide geographic range, colonies of this species are seldom recorded. This may be because of the dense coat of sand, concealed zooid openings and irregular colonies which make them inconspicuous and readily overlooked in the field.

Family RITTERELLIDAE n.fam.

The family is erected for colonial aplousobranch species with zooids either entirely embedded, or separate, the former usually organised in colonial, and sometimes rudimentary cloacal systems. Branchial and atrial openings are 6-lobed. Stigmata are in 4 or more rows. Parastigmatic vessels sometimes are present, as are branchial papillae. The oesophagus is short, and the barrel-shaped, vertical stomach has folded or smooth walls. The gonads, in a long posterior abdomen, have the ovary at the top and the male follicles usually in a longitudinal series behind the ovary. The anus opens at least half way up the atrial cavity and there usually is a distinct rectal valve at the proximal end of the ascending limb of the gut loop.

Fertilisation and incubation of embryos is in the distal (thoracic) part of the oviduct. The small (trunk length 1.0mm) larvae have 3 median, narrow-stalked eversible adhesive organs each with a small, shallow axial cone in an epidermal cup. Epidermal ampullae and vesicles suggest affinities either with *Polyclinum* (*Dumus* and the *pedunculata* group of *Ritterella*) or *Aplidium* (*aequalisiphonis* group of *Ritterella*).

Contracted zooids draw away from the surface to the base of the colony, as in Polycitoridae (see Kott 1990).

Many of the species from Australian waters (*Ritterella pedunculata*, *R. asymmetrica*, *R. multistigmata* n.sp., *R. cornuta* n.sp., *R. papillata* n.sp. and *Dumus areniferus*) have colonies like those of the *claviformis* group of *Euherdmania* (see below). Euherdmaniidae are distinguished by their long oesophagus and inverted tubular adhesive organs.

The anterior openings of the anus and the gonoducts, and (in *Ritterella dispar*) incubation of embryos in the distal (thoracic) part of the oviduct, are primitive characters shared with Placentelidae and Protopolyclinidae (e.g. *Monniotus*). The short oesophagus, and small larvae with epidermal vesicles as well as ampullae also occur in Protopolyclinidae from which *Ritterella* is distinguished by its smaller, narrower zooids with fewer male follicles in a long, thread-like or stumpy but never tapering posterior abdomen, barrel-shaped stomach with more pronounced folds and smaller, shallower adhesive organs. However, the relationship of Ritterellidae to Protopolyclinidae is not altogether satisfactorily resolved. A common diazonid ancestor is suggested by the persistence of branchial papillae in both families. The vertical stomach with longitudinally folded wall, and small larvae with shallow, stalked adhesive organs and epidermal vesicles also suggest a relationship with Polyclinidae.

Pharyngodictyon Herdman, 1886, an abyssal genus without stigmata, is represented by 6 species of which only 2 are known from a single specimen (see Millar 1982). Zooids of *P. mirabile* Herdman, 1886, *P. bisinus* Monniot and Monniot, 1991 and *P. mirabile*: Kott 1969 resemble those of some *Synoicum* spp., with a smooth, barrel-shaped stomach, and without a constriction between abdomen and posterior abdomen. However, the zooids of *P. elongatum* Millar, 1982, *P. cauliflos* Monniot and Monniot, 1991 and *P. magnifili* Monniot and Monniot, 1991 have a longitudinally folded stomach. Thus it is possible that the genus is polyphyletic despite the fact that all species have a short oesophagus, zooids opening separately to the surface, and the transverse atrial aperture at the posterior end of the dorsal surface, sometimes with both its anterior and posterior margin divided into rounded lobes (see Kott 1969). Species presently assigned to this genus are separated from Euherdmaniidae by their short gut loop, and from the Placentelidae by the position of the heart (in the posterior abdomen). The vertical, barrel-shaped stomachs are more like *Aplidium*, *Morchellium* and *Ritterella* than the oblique, dorsally shortened ones of Protopolyclinidae, Pseudodistomidae, *Polyclinum* and *Aplidiopsis*. Millar (1982) suggests a relationship between *Protoholozoa* (Holozoidae) and

Pharyngodictyon, but the presence of a posterior abdomen and the shape of the stomach does not support that view. The genus is tentatively assigned to Ritterellidae on the basis of the separately opening zooids, short oesophagus and vertical barrel-shaped stomach.

The genus *Ritterella* (with 5 or more rows of stigmata and folded stomach) is well represented in the Australian fauna. *Dumus* Brewin, 1952 (with 4 rows of stigmata and smooth-walled stomach) is known from 2 species, one possibly indigenous to the temperate waters of New Zealand and southern and eastern Australia, and one from New Caledonia.

Genus **Ritterella** Harant, 1931

Type species: *Amaroucium aequalisiphonis* Ritter and Forsyth, 1917.

The genus contains embedded zooids opening independently, and sometimes organised in colonial systems. Colonies are often, but not always, brittle with sand. The stomach has longitudinal folds in its wall, sometimes shallow and inconspicuous but well defined in other species.

The species of *Ritterella* with parastigmatic vessels are *R. tokioka* nom. nov. and *R. yamazii* Tokioka, 1949 from Japan, *R. arenosa* (Brewin, 1950) from New Zealand, *R. circularis* Monniot, 1987 from New Caledonia, and *R. asymmetrica* and *R. multistigmata* n.sp. from Australia. Kott (1972a) proposed that the presence of 5 primary rows of stigmata (which sometimes are bisected by parastigmatic vessels) is characteristic of *Ritterella*. However, although 5 primary rows occur in many species it is not universal.

The type species *R. aequalisiphonis* (Ritter and Forsyth, 1917) from California was assigned to *Sigillinaria* Oka, 1933 by Van Name (1945), who, like Millar (1960), believed the genera synonymous. However *Sigillinaria* is a synonym of *Placentela* Redikorzev, 1913 (see above). *Distoma pulchra* Ritter, 1901 (*Sigillinaria pulchra*: Van Name, 1945) has a folded stomach, but long oesophagus, and despite its embedded zooids, is more like *Euherdmania* than *Ritterella*.

Most of the species of *Ritterella* can be assigned to one of 2 species groups, viz.:

(1) *Aequalisiphonis* group, containing *R. prolifera* (Oka, 1933), *R. dispar* Kott, 1957, *R. tokioka* nom. nov. (for *R. pedunculata* Tokioka, 1953), *R. sigillinoides* (Brewin, 1958) and *R. glareosa* Monniot, 1974, as well as the type species of the genus. These naked or sandy colonies sometimes are stalked, the zooids are not arranged in distinct systems, and the short, thick posterior abdomina have bunched male follicles. The known larvae (of *R. dispar*, *R. prolifera* and *R. glareosa*) have epidermal vesicles separating directly from the epidermis like larvae of certain *Aplidium* spp. (see Fig. 60).

(2) *Pedunculata* group, containing *R. pedunculata* (Herdman, 1899) and 5 other sandy species, *R. papillata* n.sp., *R. asymmetrica* Millar, 1966, *R. multistigmata* n.sp., *R. cornuta* n.sp., *R. compacta* n.sp., from Australian waters. All have zooids arranged in systems, with sandy, usually narrow-stalked colonies (*R. compacta* excepted), long, narrow posterior abdomina with male follicles in longitudinal series, and larvae with postero-ventral and dorsol vesicles, and anterior ampullae like *Polyclinum*. The naked *Ritterella circularis* Monniot, 1987 from New Caledonia is also a member of this group of species; and *R. yamazii* Tokioka, 1949 from Japan may be.

The known larvae have ectodermal ampullae and clusters of vesicles like those of *Polyclinum*.

Ritterella arenosa (Brewin, 1950) and *R. vestita* Millar, 1960 do not appear to have affinities with either of the species groups (see below). Nevertheless, *Ritterella* appears to be monophyletic.

Ritterella rubra Abbott and Trason, 1958 from California lacks systems, has zooids opening separately to the exterior but has a mulberry-like stomach and curved oesophagus. The species appears to have a similar relationship with *Synoicum* to that of *Ritterella* with *Aplidium*.

Seven species of *Ritterella* are known from Australian waters, 5 from the temperate waters of the southern coast, where the genus appears to have radiated (Table 3). These and other aplousobranch species with separately opening zooids (e.g. *Dumus areniferus*, *Monniotus* spp., and *Condominium areolatum* n.gen.) appear to flourish in the same sandy coastal habitats.

Key to species of *Ritterella* recorded from Australia

1. Lobes of colony long and narrow 2
   Lobes of colony not long and narrow 6
2. Stigmata in 5 rows 3
   Stigmata in more than 5 rows 5
3. Parastigmatic vessels present ..... *R. asymmetrica*
   Parastigmatic vessels not present 4

4. Branchial papillae present ..... *R. papillata* n.sp.
   Branchial papillae not present .. *R. pedunculata*

5. Parastigmatic vessels present .....
   .....*R. multistigmata* n.sp.
   Parastigmatic vessels not present .....
   .....*R. cornuta* n.sp.

6. Colony sandy; zooids in systems .....
   .....*R. compacta* n.sp.
   Colony not sandy; zooids not in systems .....
   .....*R. dispar*

Species recorded from regions other than Australia.

In addition to the species recorded from Australia, which are all indigenous, the genus is known from the eastern Pacific (southern California) by the type species, and from New Zealand and Japan by the following:

Ritterella arenosa (Brewin, 1950) from New Zealand (Great Barrier I. and Hauraki Gulf; see also Brewin 1958). Despite its smooth stomach (which occurs also in *Dumus*) the species, with its zooids embedded (rather than separate) in sandy flat-topped lobes, parastigmatic vessels (like *R. asymmetrica*), 9 or 10 rows of 20 to 24 stigmata, and narrow posterior abdomen with the ovary in front of the longitudinal series of testis follicles, seems most appropriately assigned to *Ritterella*. It shares some characters with *Homoeodistoma longigona* Tokioka, 1959, although the latter species seems to have closer affinities with the Diazonidae (see above, Placentelidae).

Ritterella circularis Monniot, 1987 from New Caledonia has circular systems with the atrial apertures in a central depression as in *R. compacta* n.sp. The species also has a similar number of rows of stigmata. Unlike *R. compacta* its colony is not sandy, has more stigmata per row, has parastigmatic vessels, and lacks branchial papillae.

Ritterella glareosa Monniot, 1974, from 300m on a sea-mount in the northern Pacific, is thought isolated there. The spherical, sand-encrusted species has 5 to 7 rows of numerous stigmata, and the usual slender muscle bands extend the whole length of the body. Testis follicles are bunched, but this could be the result of contraction of the posterior abdomen. They are not as numerous as they are in Protopolyclinidae. As in other species, the rectum and gonoducts extend at least halfway up the atrial cavity, and there is a rectal valve at the proximal end of the ascending limb of the gut loop. The stomach has 5 faint longitudinal folds. The larvae have ectodermal vesicles but no ampullae, and there is an otolith but no ocellus. The species is distinguished from others by the form of its colony and the number of faint stomach folds. The embryos probably are incubated in the distal part of the oviduct, as are the embryos of *R. dispar* and *R. prolifera*, from which the present species is distinguished by its sand encrusted colony, and fewer stomach folds.

Ritterella prolifera (Oka, 1933) from Japan (see Tokioka 1953) closely resembles *R. dispar*, differing from it only in having 6 (rather than 5) rows of stigmata.

Ritterella sigillinoides (Brewin 1958) from Stewart I. has a fleshy stalked colony without sand, no systems, zooids with 5 rows of stigmata, a folded stomach and

TABLE 3. Summary of characters of species of *Ritterella* recorded from Australia

Species	Biogeographic range[1]	Range anticlockwise around Australia	Colony	Systems	Stigmata: no. rows; no/row	Parastigmatic vessels	Branchial papillae	Stomach folds
R. compacta n.sp.	A,te	Gt Australian Bight	sandy, compact cushion	rudimentary cloacal	15;20	absent	10	6
R. cornuta n.sp	A,te	"	sandy stalks	"	9;15–20	absent	15	6+
R. papillata n.sp.	A,te	"	"	"	5;15	absent	15	8
R. pedunculata	A,te	Gt Australian Bight to Solitary Is (NSW)	"	colonial	5;12	absent	0	4–5
R. assymmetrica	A,te	Gt Australian Bight to Port Phillip Bay	"	"	5;20	present	0	15
R. dispar	IWP,tr	NSW to Mackay	naked lobes	none	5;16	absent	0	15

[1] A, indigenous; IWP, Indo-West Pacific; te, temperate; tr, tropical.

neither branchial papillae nor parastigmatic vessels. Colonies superficially resemble *R. prolifera* or *R. dispar*, but these species are sessile, and lack the narrow stalk of the present one.

Ritterella tokioka nom. nov. for *R. pedunculata* Tokioka, 1953 from Japan has 12 rows of stigmata, each crossed by parastigmatic vessels, a short oesophagus and folded stomach. The colonies are stalked heads arising from a basal stolon resembling those of *R. sigillinoides* from New Zealand, but the zooids differ.

Ritterella vestita Millar, 1960 from the North Island, New Zealand. This species has a sandy, stalked head, without systems, zooids with 27 to 34 rows of 40 to 50 stigmata, a folded stomach, and testis follicles in a longitudinal series. It lacks both parastigmatic vessels and branchial papillae.

Ritterella yamazii Tokioka, 1949 from Japan is a soft semitransparent cushion with 5 rows of stigmata with parastigmatic vessels, 10 stomach folds, 2 rows of testis follicles, and epidermal vesicles in the larval test.

Ritterella sp. aff. *aequalisiphonis*: Tokioka, 1967 from Japan, has 14 rows of stigmata. Its naked, clavate colonies distinguish it from most Australian species.

Ritterella asymmetrica Millar, 1966
(Fig. 4. Plate 1e,f)

Ritterella asymmetrica Millar, 1966, p. 361.

DISTRIBUTION
NEW RECORDS: South Australia (Great Australian Bight, SAM E2102 E2104, QM GH4157 GH4195 GH4930; Kangaroo I., QM GH5427; Cape Jaffa, QM GH5445). Victoria (Nelson Bay, MV F57792).
PREVIOUSLY RECORDED: Victoria (Port Phillip — MV H39 Millar 1966).

DESCRIPTION
EXTERNAL APPEARANCE: Colonies consist of upright, sandy, cylindrical to flattened stalks up to 4cm long, branching along their length, with terminal more or less club-shaped but bilaterally symmetrical expansions up to 1cm long and 6mm wide. On one side, the long terminal expansion is slightly flattened, with a scalloped margin. On the other, it is deeply convex. The atrial apertures open around the outside (deeply convex side) of the scalloped margin, and the branchial apertures

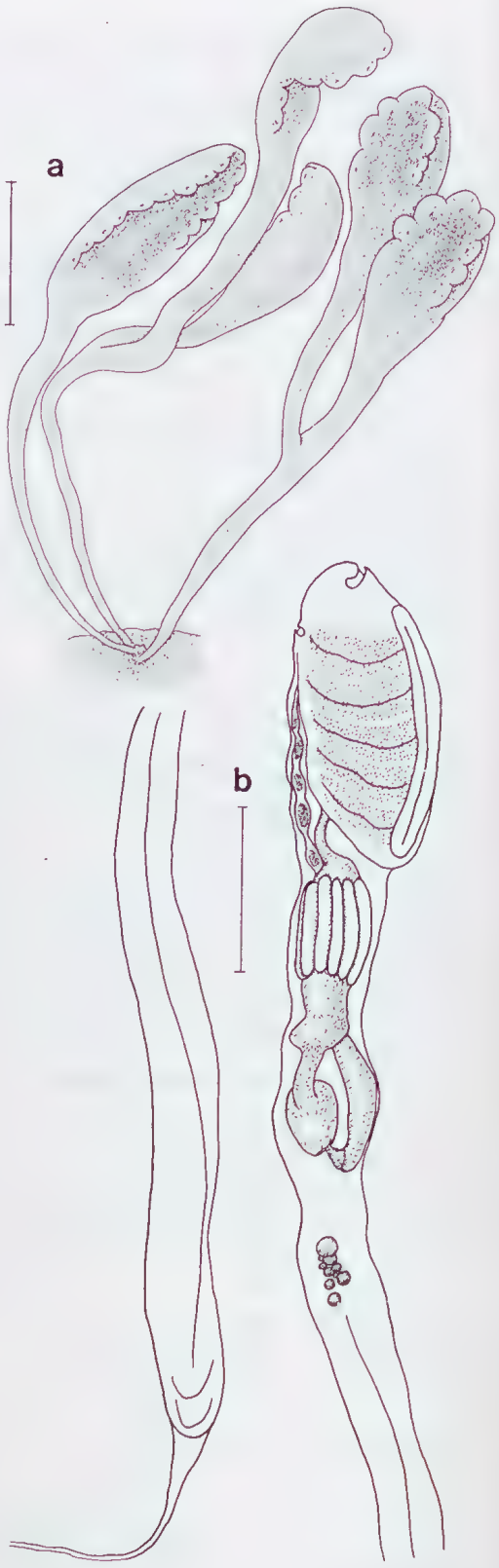


FIG. 4: *Ritterella asymmetrica* (MV F57792) — **a**, part of colony; **b**, zooid (posterior half of posterior abdomen shown separately). Scales: **a**, 1cm; **b**, 1mm.

are in a groove around the other (flat) side. Sand covers the outside of each stalk but is absent from the delicate internal test. In some of the preserved specimens the internal terminal expansion is spoon-shaped, its flat side slightly concave. In life it is probably slightly convex, presented to oncoming currents, deflecting the current past the branchial apertures that surround it.

The scalloped margin around the free end of each lobe is formed by the surface test swelling over the anterior end of each zooid. Each lobe of the colony contains up to 16 zooids, arranged parallel to one another in a single layer.

INTERNAL STRUCTURE: Zooids are about 1cm long, with thorax and abdomen of more or less equal length, and a longer, thread-like posterior abdomen. Both apertures are sessile, transversely elongated, and the 6 lobes around the rim of each opening are minute, sharply pointed and widely separated from one another, 3 on each facing lip. The branchial aperture is terminal and bent ventrally, the atrial sub-terminal and directed dorsally. A sphincter muscle is present around each aperture. A layer of fine transverse thoracic muscle fibres surrounds the slender longitudinal muscles which extend from the thorax onto the abdomen. Each of the 5 rows of about 20 long, narrow, parallel stigmata, is crossed by a conspicuous parastigmatic vessel. The transverse vessels are wide membranes projecting into the lumen. When contracted the edges of these membranes are drawn into tight frills that superficially resemble branchial papillae. However branchial papillae are not present. Triangular dorsal languets are on parastigmatic vessels as well as on primary transverse vessels.

The short, barrel-shaped stomach is in the anterior half of the abdomen. Twelve to 15 longitudinal folds are in its parietal wall, but the surface of the mesial wall is irregular. A long duodenal area, mid-gut and oval posterior stomach occupy the remainder of the descending limb of the gut loop. The rectum extends halfway up the thorax to open in a bilabiate anus just behind the atrial aperture. A small ovary with up to 12 small eggs is in the anterior part of the posterior abdomen. Mature testis are not present in any of the newly recorded South Australian and Victorian specimens (collected in April and June respectively), although they are present in the type specimen in 2 irregular longitudinal series (Millar 1966).

REMARKS

Millar (1966) believed that the branchial sac contained 10 rows of stigmata rather than 5, misinterpreting the parastigmatic vessels. These are true parastigmatic vessels, with the long stigmata continuous beneath them. The number of stigmata is difficult to determine in contracted specimens, but although at least 20 were counted there do not seem to be as many as the 35 Millar (1966) recorded.

Kott (1972a) discussed the possibility of this species being conspecific with *R. pedunculata*, suggesting that differences between the 2 species, viz. the size of colonies, zooids and branchial sacs, could be associated with growth. However, growth and maturity of *R. pedunculata* is not associated with increases of the order that could explain the differences. Although very large colonies of *R. pedunculata* have been examined, they all consist of the characteristically narrow lobes with not more than 12 zooids, and short stigmata without parastigmatic vessels. Further, the colonies are different, for atrial apertures of *R. asymmetrica* open around the convex sides of a club-shaped terminal expansion to form systems homologous with those of *Condominium areolatum* (see above); while those of *R. pedunculata* open in a row onto the concave side of a flat, fan-shaped expansion to form analogues of cloacal systems (see *R. cornuta* n.sp., below).

Transverse apertures with widely separated minute lobes on their rims are found in *Monniotus* spp., although, no phylogenetic relationship is implied by this. Rather the arrangement is an adaptation associated with the openings on opposite sides of the colony (see Kott 1989).

Ritterella compacta n.sp.
(Fig. 5. Plate 2a,b)

DISTRIBUTION

TYPE LOCALITY: South Australia (Investigator Group, Flinders I., in caves, coll. N. Holmes 10.4.83, holotype QM GH2399 *SAM E2094*; eastern side of Grindle I., 10-15m, coll. W.H. Sasse, 7.4.87 paratype, QM GH4172 *SAM E2095*; Price I., 15-20m, coll. N. Holmes 9.4.87, paratype QM GH4177 *SAM E2096*).
FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are compact, sessile, and hemispherical to almost spherical, with the surface either undivided or (QM GH4177) subdivided into tightly packed cylindrical lobes, each containing a single circular system of 6 to 8 zooids. The test is sandy throughout and the zooids are in rigid, vertical compartments. The branchial openings are in circular depres-

sions, around the periphery of the rigid sandy swellings or lobes (almost 5mm diameter) on the surface of the colony. Atrial openings are in a depression of varying depths in the centre of each lobe. Sometimes the central depression is deeper and forms a rudimentary cloacal cavity (QM GH2399 GH4172), opening to the surface through a central aperture and receiving the atrial openings of the zooids that surround it. A layer of sand continuous with the layer encrusting the outside of the colony lines the inside of the rudimentary cloacal cavity. It is homologous with the simple depression in the less compact colony (QM GH4177).

FIG. 5: *Ritterella compacta* n.sp. — **a**, diagrammatic cross section through a system (holotype QM GH2399); **b**, whole zooid (paratype QM GH4177); **c**, **d**, zooids (holotype QM GH2399); **e**, atrial siphon showing extended dorsal rim of aperture and dorsal median papilla (holotype QM GH2399). Scales: **b–d**, 1mm; **e**, 0.2mm.

INTERNAL STRUCTURE: The zooids are about 1cm long, they have a long thorax, a slightly shorter abdomen and a posterior abdomen that varies from about half to one third of the total zooid length. The 6-lobed branchial aperture is terminal, and the large atrial siphon subterminal. Often the anterior rim of the atrial siphon is produced into a lip of various lengths. The tip of the lip is divided into 3 pointed lobes, and the lower (posterior) half of the rim of the atrial aperture has another 3 widely separated small, pointed, lobes. In some zooids a pointed projection, or papilla projects from the dorsal mid-line on the posterior wall of the atrial siphon.

Circular muscles are present around the branchial and atrial apertures, curving out along the anterior atrial lip when one is present. About 12 longitudinal muscles extend down the thorax from each of the siphons. Posteriorly they extend along each side of the abdomen and posterior abdomen. Atrial lips are inserted into the rim of cloacal depressions or into the margin of cloacal apertures, so that the zooids in each system provide some muscular control around the rim of the opening.

Sixteen rows of about 20 stigmata are separated from one another by transverse vessels with about 14 rounded papillae on each. The stomach, with about 6 longitudinal folds on the parietal wall and irregular creases on the mesial wall, is about halfway down the abdomen. There is a duodenum and a mid-intestine in the descending gut loop. A distinct rectal valve is present at the proximal end of the ascending limb of the gut loop.

Gonads are in the upper half of the posterior abdomen, the 3 or 4 egg ovary anterior, and behind it almost spherical male follicles are bunched together.

REMARKS

Variations in length of atrial lip and the shape of the dorsal median papilla (on the posterior wall of the siphon) probably result from muscular action. With the exception of those variations, the zooids in the 3 available colonies of this species

have the same characters. However, the colonies are more variable. The compact colonies with rudimentary cloacal systems superficially look very different from the one with its upper surface divided into lobes and with cloacal depressions rather than cavities. Nevertheless, these seem to be differences of degree rather than definitive morphological differences.

The species demonstrates the close relationship between forms without, and others with, true cloacal systems. Despite the variations in the development of separate lobes, this species does not have the same capacity to respond to changes in prevailing currents as the stalked *Ritterella*.

The rudimentary cloacal system is a unique feature in this genus. It has not been observed in other *Ritterella* spp; although it parallels certain species of *Eudistoma* (e.g. *E. angolanum*, *E. carnosum*, *E. reginum*: see Kott 1990). The branchial sac with its branchial papillae and numerous rows of stigmata resembles that of *Ritterella cornuta* n.sp.

Ritterella cornuta n.sp.
(Fig. 6. Plate 2c)

DISTRIBUTION
TYPE LOCALITY: South Australia (Price I., coll. W.H. Sasse 9.4.87, holotype QM GH4176 *SAM E2098*).
FURTHER RECORDS:None.

DESCRIPTION
EXTERNAL APPEARANCE: The colony consists of narrow, sandy stalks about 2cm long and 0.4cm in diameter attached basally to branching stolons. Terminally they are divided into 2 or 3 flattened, fan-shaped expansions, and have 2 or 3 branches along their length. The terminal flattened part of each lobe has a median depression. This depression receives the atrial apertures of the zooids which are arranged in a row along each side of the depression. The branchial apertures are along the outside of the rounded rim along each side of the median depression. Sand forms a dense coat around the outside of the colony and there is some embedded in the internal test.

INTERNAL STRUCTURE: The zooids are about 1cm long. Thorax and abdomen together represent slightly more than half the length of the zooid. Each aperture has 6 pointed lobes. The branchial aperture is terminal, oriented slightly ventrally, and the atrial aperture, on a short siphon

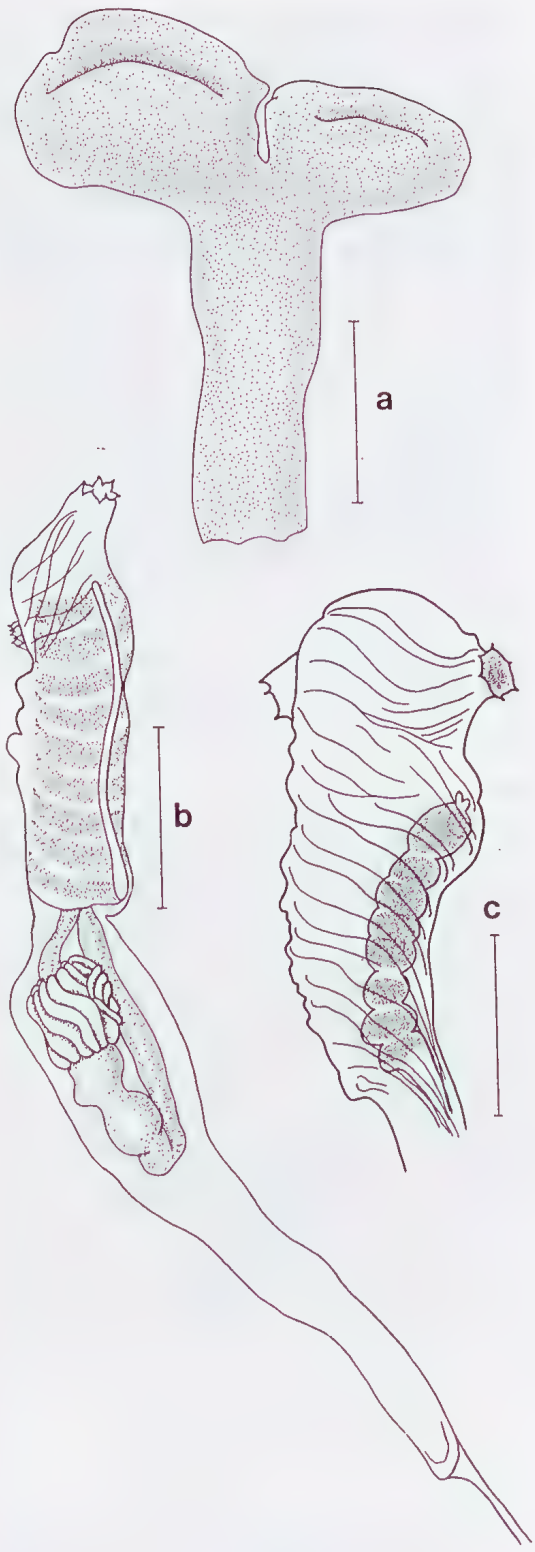


FIG. 6: *Ritterella cornuta* n.sp. (holotype QM GH4176) — **a**, part of colony; **b**, zooid; **c**, thorax. Scales: **a**, 5mm; **b**, **c**, 1mm.

directed at right angles to the long axis of the zooid, is about one quarter of the thorax length along the dorsal surface.

The body musculature is longitudinal and oblique, although in the examined zooids most bands extend transversely across each side to the dorsal surface before running the length of the zooid. About 5 bands are from the branchial siphon and a further 12 are from the endostyle. The muscles extend onto the abdomen and posterior abdomen from each side of the dorsal mid-line of the thorax. Stigmata are arranged in 9 rows of about 15 to 20. About 2 rounded papillae to every 3 stigmata are on the transverse vessels. There are no parastigmatic vessels.

The abdomen is relatively short, the stomach about halfway down, with about 6 indistinct oblique folds on the parietal surface, but with irregular creases on the side facing the ascending limb. A short duodenum and mid-intestine are in the descending limb distal to the stomach. The rectum extends about halfway up the thorax, terminating in a bilabiate anus. Gonads are not present in these specimens. The heart is present in the posterior end of the posterior abdomen.

Remarks

The species most closely resembles *Ritterella papillata* n.sp., which has similar although narrower colonies and forms rudimentary cloacal systems. The latter species has smaller zooids with only 5 rows of stigmata and is thus distinguished from the present species. The colonies of both resemble those of *R. pedunculata*, but the latter species lacks branchial papillae and has a bilaterally symmetrical concavity at one side, rather than a radially symmetrical one on the free end of the lobe surrounded by zooids, as it is in the present species and *R. papillata* n.sp. Nevertheless, these concavities in *R. cornuta*, *R. papillata* n.sp. and *R. pedunculata* all serve to concentrate the excurrent streams of water and separate them from the incurrent streams. *Ritterella asymmetrica* is different, the atrial openings being around the convex side of the terminal expansion (see *Condominium areolatum*, above).

Ritterella dispar Kott, 1957
(Fig. 7. Plate 2d)

Ritterella dispar Kott, 1957, p. 102; 1963, p. 78. Monniot and Monniot, 1976, p. 360.
Ritterella proliferus: Kott, 1972c, p. 245; 1981, p. 157 (part, specimen from Lord Howe I.).

Distribution

New Records: Queensland (Moreton I., QM GH4940; Noosa, QM G4969; Capricorn Group, QM G9468 GH881 GH4941–4 GH4947–8 GH4950–1).
Previously Recorded: New South Wales (Arrawarra QM GH5588). Queensland (Caloundra — AM U3897 Kott 1957; Currumbin — Kott 1963; Moreton Bay, Hervey Bay, Noosa Heads; Sarina — AM Y1116 Kott 1963). Lord Howe I. (QM G12001 Kott 1981). West Indian Ocean (Mauritius — Monniot and Monniot 1976).

The species is very common in the intertidal region on the mid-eastern coast of Australia and the southern part of the Great Barrier Reef. It has not been taken from the western Pacific — reexamination of the specimen from Fiji, which Kott (1981 QM GH102) assigned to *R. proliferus*, has shown it to be an *Aplidium* sp.

Description

External Appearance: Small flat-topped sessile cushions, sometimes lobed, and round to polygonal in outline, form mosaics on hard substrates. They are attached by the centre of the flat basal surface. The relatively thick, but fairly short evenly spaced zooids open on the flat upper surface. Colonies are one or 2cm in maximum extent, and never more than 1cm thick. When expanded, the crowded colonies appear to be continuous with one another, but when either contracted or preserved they are seen to be separate. In life they are a flesh colour, with white zooids showing through, or 'ochraceous buff' (Ridgeway 1886) with iridescent blue zooids.

Internal Structure: Zooids are relatively short (about 5mm) but quite thick, with a short posterior abdomen, and a wide thorax. Apertures are both anterior, each surrounded with 6 pronounced lobes. The lobes of the atrial aperture are particularly long, petal-like, and sometimes divided into 2, although those of the branchial aperture are shorter and triangular. Sphincter muscles are present around the base of each siphon. About 15 fine, parallel longitudinal muscles are on the thorax, and extend along the ventral side of the abdomen and posterior abdomen. Transverse muscles were not detected. There are 5 rows of 16 stigmata. Neither parastigmatic vessels nor branchial papillae are present. The oesophagus is short, and the stomach broad, with 15 parallel longitudinal folds. There is a broad duodenal region. An oval posterior stomach is in the bend of the gut loop. It is separated from duodenum and rectum by narrow mid-intestinal constrictions. A rectal valve is at the base of

the ascending limb. Both gonoducts and anus open in the anterior part of the atrial cavity, near the base of the atrial siphon. The anal border is bilabiate. Gonads are in the short, stumpy posterior abdomen, the testis follicles in a more or less spherical clump, surrounding the ovary.

Specimens taken in May and August from the Capricorn Group (QM GH4941 GH4947) and in May from Noosa (QM GH4969) contained embryos. Embryos were not present in specimens taken from the Capricorn Group in February and April.

Each zooid contains one (QM GH4969) to 3 (QM GH4947) embryos or infertile eggs serially arranged in the distal (thoracic) part of the oviduct. Only the most anterior egg appears to mature to a tailed larva, and it is possible that the other eggs may be infertile. In specimens from Noosa (QM GH4969) there is a single tailed larvae in the distal end of the oviduct with what appears to be an infertile egg just behind it.

In one colony, the larval trunk varies in length from 0.6 to 0.8mm. It has the tail wound three-quarters of the way around it. The 3 median adhesive organs have wide shallow cones of secretory cells, and narrow stalks. Seven to 9 large epidermal vesicles in a row on each side are scattered around the adhesive organs as the larva matures. An ocellus and an otolith are in the cerebral vesicle.

Remarks

These elegant transparent cushion-like colonies with independently opening zooids are significantly different from the colonies of other *Ritterella* spp. recorded from Australia, with their narrow sandy stalks and zooids arranged in colonial systems. There also are differences in the zooids, those of the present species being similar

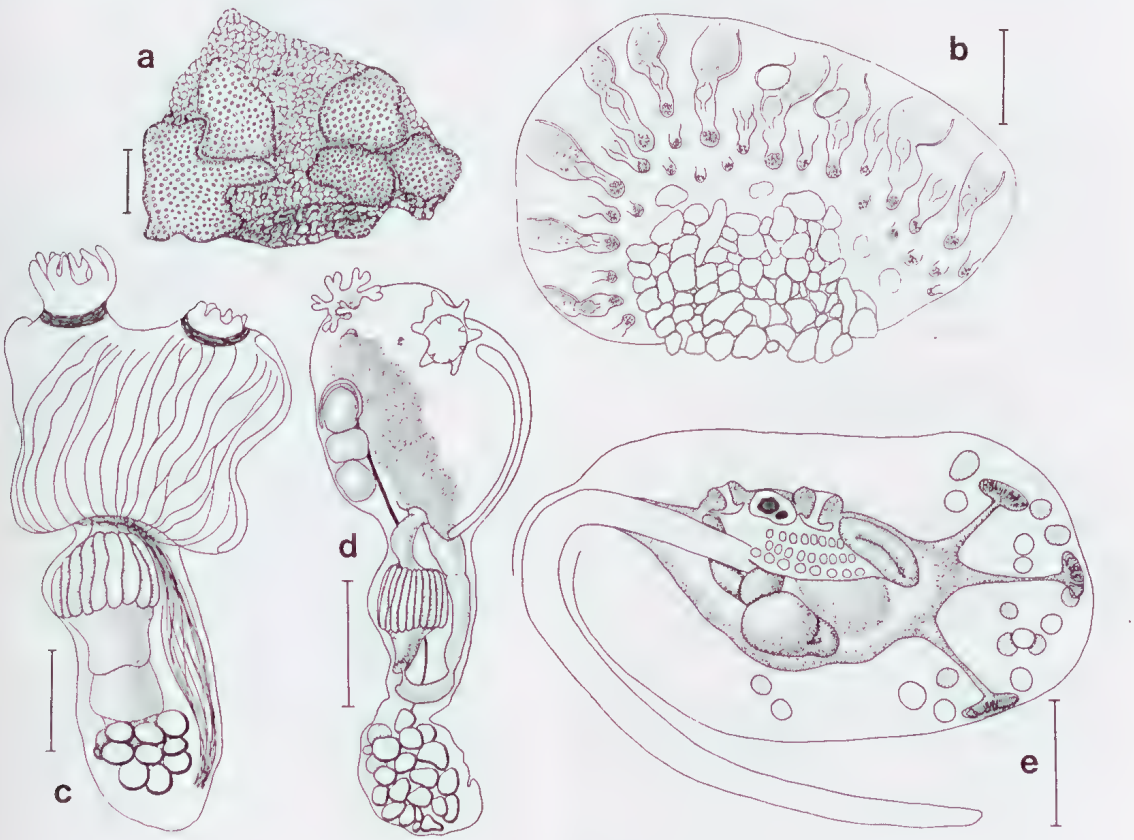


FIG. 7: *Ritterella dispar* — **a**, colonies viewed from above (QM GH4969); **b**, zooids seen in margin of colony viewed from below (QM GH4951); **c**, **d**, zooids (**c**, QM GH4951; **d**, QM GH4943); **e**, larva (holotype AM U3897). Scales: **a**, 1cm; **b**, 2mm; **c**, **d** 1.0mm; **e**, 0.2mm.

to others of the *aequisiphonalis* group, while zooids of other Australian species belong to the *pedunculata* group.

The relationship between *R. prolifera* (Oka, 1933) from Japan (see Tokioka 1953, Nishikawa and Tokioka 1976) and the present species is also very close, the only difference detected being the 6 rows of stigmata in the Japanese species as against 5 in *R. dispar*. Both species have deep, petal-shaped and sometimes bifid atrial lips, fine longitudinal body muscles, a short stomach with parallel folds, short posterior abdomen with bunched male follicles, up to 3 eggs in the distal end of the oviduct, and an identical larval trunk with a row of large, spherical ampullary vesicles each side of the adhesive organs, but no ectodermal ampullae. The colonies also are very similar, *R. prolifera* having the same flat, cushion-like, whitish, iridescent colonies that form mosaics on hard substrate and weed. On the basis of these similarities, Kott (1969, 1972d) proposed the synonymy of *R. dispar* and *R. prolifera*. They are presented here as separate species solely on the basis of the difference in the number of rows of stigmata.

The lack of continuity in the geographic range of the present species, with populations in Mauritius (Monniot and Monniot 1976) and on the sub-tropical coast of eastern Australia, is puzzling. There are no records from further north than Mackay, despite the fact that the species is common on the central coast. It is probable that the West Indian Ocean populations are isolated from the Australian ones.

Ritterella multistigmata n.sp.
(Fig. 8. Plate 2e)

DISTRIBUTION

TYPE LOCALITY: Western Australia (Sisters Reef, Murray Reef Warnbro Sound near Rockingham, 46°21.3S 115°41.3E, coll. AIMS Bioactivity Group 22.3.89, holoytpe QM GH5463).

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: The holotype colony is a large one, consisting of long (to 7cm), narrow (to 4mm diameter) sandy stalks, branched up to 3

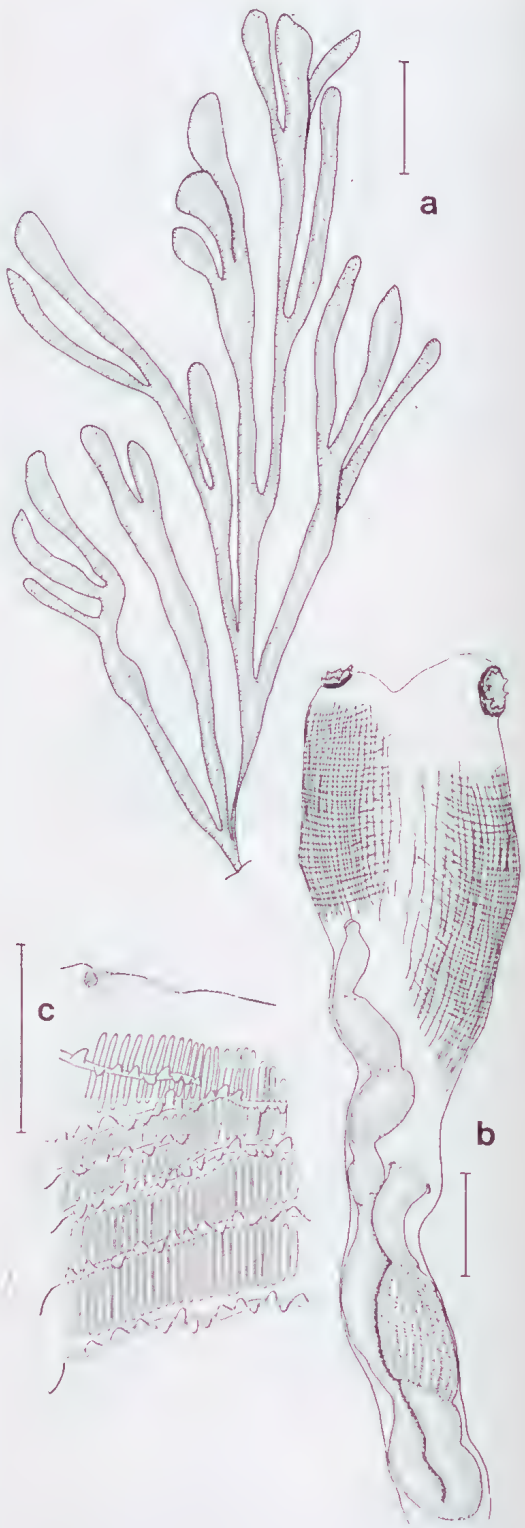


FIG. 8: *Ritterella multistigmata* n.sp. (holotype QM GH5463) — **a**, part of colony; **b**, thorax and abdomen; **c**, portion of branchial sac showing the neural gland and its opening, transverse and parastigmatic vessels, dorsal languets, and branchial papillae. Scales: **a**, 1cm; **b**, 1mm; **c**, 0.5mm.

times along their length. The terminal free ends are slightly expanded club-, or spoon- or fan-shaped. Each contains one to 3 zooids. Sand is crowded on the outer surface and is embedded in the surface layer of test making it brittle. However there is no sand internally, where zooids are in narrow longitudinal compartments in the transparent but tough test.

The long branching stalks of the colony are parallel to one another, and are crowded together to form compact masses.

INTERNAL STRUCTURE: Zooids are long and delicate, extending from the free end of a terminal lobe to the base of the colony. Most of that length is the narrow, thread-like posterior abdomen. The thorax and abdomen are together about 9mm long, with the abdomen about two-thirds the length of the thorax. The branchial aperture is turned ventrally, and the atrial aperture is directed anteriorly. Each of the apertures has 6 small points around the rim.

The thoracic body wall has an open meshwork of fine longitudinal and transverse muscle bands. Only the longitudinal bands extend to the posterior end of the zooid. The branchial sac has 10 rows of long, narrow stigmata each row crossed by a sturdy parastigmatic vessel which appears to be further subdividing the row of stigmata. Each transverse and parastigmatic vessel has about 12 large conspicuous rounded papillae evenly spaced along it. There are large triangular dorsal languets on parastigmatic as well as on primary transverse vessels. About 35 stigmata per row are in the rows about halfway down the pharynx, but fewer anteriorly, and even fewer posteriorly. Sixteen stigmata are in the most posterior row.

The long, oval stomach is halfway down the abdomen. The stomach wall is smooth externally but has fine longitudinal ridges internally. The post-pyloric part of the gut is wide, and has no marked divisions. The bilabiate anus opens about halfway up the branchial sac.

Gonads are not developed in this specimen.

REMARKS

Although they seem to branch more, the sandy stalks of this species with their asymmetrical tips most resemble those of *Ritterella pedunculata* and *R. asymmetrica*. Other *Ritterella* spp. have similar sandy stalks but radially symmetrical tips. Nevertheless *Ritterella cornuta* and *R. papillata* n.sp. are the only other stalked species that have numerous branchial papillae on the transverse vessels. However, both species lack parastigmatic vessels, *R. papillata* n.sp. has only 5 rows of stigmata, and although *R. cornuta* has a similar number of rows of stigmata (9) to the present species, it has a folded stomach wall rather than internal ridges. *Ritterella compacta* also has numerous rows of stigmata and branchial papillae, stomach folds, an atrial siphon with a long anterior lip adapted for circular colonial systems, and a compact colony, but it lacks parastigmatic vessels.

The unique characters of the present species are its branchial papillae, parastigmatic vessels, internally ridged stomach, and fine meshwork of longitudinal and transverse muscles on the thorax.

Ritterella papillata n.sp.
(Fig. 9)

DISTRIBUTION

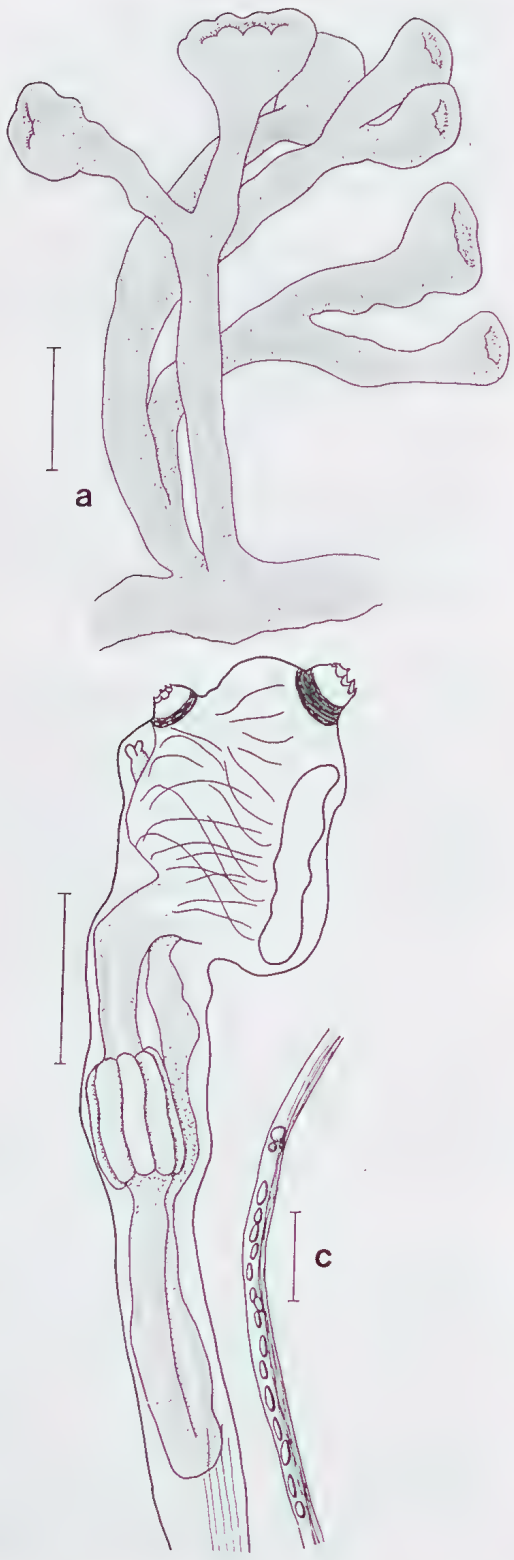
TYPE LOCALITY: South Australia (Price I., coll. W.H. Sasse 9.4.87, holotype QM GH4148 *SAM E2097*; Taylor I., coll. W.H. Sasse 6.4.87, paratype QM GH4217).
FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: The colonies consist of a tangle of narrow, sandy stalks up to 5cm long, with a terminal inverted conical expansion, concave on the free end. The atrial apertures open around the inside of the terminal concavity and the branchial apertures are in a single circle around the outside of its rounded margin. The sandy test is sometimes raised in rounded swellings over the anterior end of each zooid. Up to 10 zooids are in each lobe. The terminal concavities often are turned to the side, presumably facing away from the oncoming current, which, as it passes the colony, probably entrains the excurrent stream of water (see Kott 1989).

INTERNAL STRUCTURE: Zooids are long and thread-like, with a long posterior abdomen that is up to 3cm long — many times the length of the thorax and abdomen together (about 2mm). There are black pigment cells scattered in the body wall. Each aperture has 6 small sharply pointed lobes. The branchial aperture is terminal, turned slightly ventrally. The atrial aperture is about one-third of the distance down the dorsal surface of the thorax. About 20 thoracic muscles are oblique (from the branchial siphon to the dorsal surface) and transverse (from the ventral mid-line), joining into bands along each side of the abdomen and posterior abdomen.

In the branchial sac about 15 stigmata are present in each of 5 rows. The transverse vessels have flat, rounded papillae, containing dark black



pigment, about one to each stigma, along their edge. There are no parastigmatic vessels. The short stomach lies halfway down the abdomen. It has 6 broad but faint, oblique, parallel folds on the parietal wall, but its mesial wall is smooth. The bilabiate anus is halfway up the branchial sac. The gonads are in the posterior half of the posterior abdomen the small (about 3-egg) ovary anterior to a single longitudinal series of male follicles. In the type specimens, there are 4 or 5 embryos in the atrial cavity, but these do not include tailed larvae.

REMARKS

Although the colonies of *R. cornuta* are similar, those of the present species are narrower, and the terminal expansion is less flattened and not so wide. The zooids of the present species are smaller, with fewer rows of stigmata but much longer posterior abdomina. The accumulations of black pigment in the branchial papillae are not present in *R. cornuta*. *Ritterella pedunculata* and *R. asymmetrica* differ in not having branchial papillae. The terminal depressions containing the atrial openings are homologous with those of *R. cornuta* (see *R. cornuta* n.sp. REMARKS) and *R. compacta* n.sp. They are also radially symmetrical like those of *R. cornuta*, not bilaterally symmetrical like *R. pedunculata*.

Ritterella pedunculata (Herdman, 1899)
(Fig. 10. Plate 2f,g)

Psammaplidium pedunculatum Herdman, 1899, p. 88.
Not *Ritterella pedunculata* Tokioka, 1953, p. 184 (*R. tokioka* nom. nov.).
Ritterella herdmania Kott, 1957, p. 102 (part specimens from NSW); 1963, p. 78; 1972a, p. 11 (part); 1972b, p. 172; 1975, p. 2.

DISTRIBUTION

NEW RECORDS: South Australia (Great Australian Bight, SAM E2417; Spencer Gulf, QM GH1823 GH4927; St. Vincent Gulf, QM G9323; Margaret Brock Reef, SAM E2101; Cape Northumberland QM GH4928–9). Tasmania (Bruny I., MV F57793; St. Helens, QM G10156). Victoria (90 ml Beach, QM G12713; Portland, QM GH95; Port Phillip Bay, QM G10160 GH4682; Westernport, MV F57790 F57794). New South Wales (Port Hacking, AM Y2170; North Solitary I., QM G9642; Arrawarra, QM GH5393).

FIG. 9: *Ritterella papillata* n.sp. (holotype QM GH4148) — **a**, part of colony; **b**, thorax and abdomen; **c**, part of posterior abdomen with gonads. Scales: **a**, 5mm; **b**, 0.5mm; **c**, 2mm.

PREVIOUSLY RECORDED: South Australia (Great Australian Bight — SAM E2105–10 QM G9292 Kott 1972b, 1975; St. Vincent Gulf — SAM E2450 Kott 1972a). New South Wales (Port Hacking, Newport — AM U3862 U4017 Y821 Y1131 Y2170 Kott 1957, 1963; Port Jackson — Herdman 1899).

Specimens are from depths to 12m, often in fast-flowing currents. The species is very common in Port Phillip Bay.

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are sometimes very large tangles of thin, sandy, branching stalks, one to 6cm long, attached to

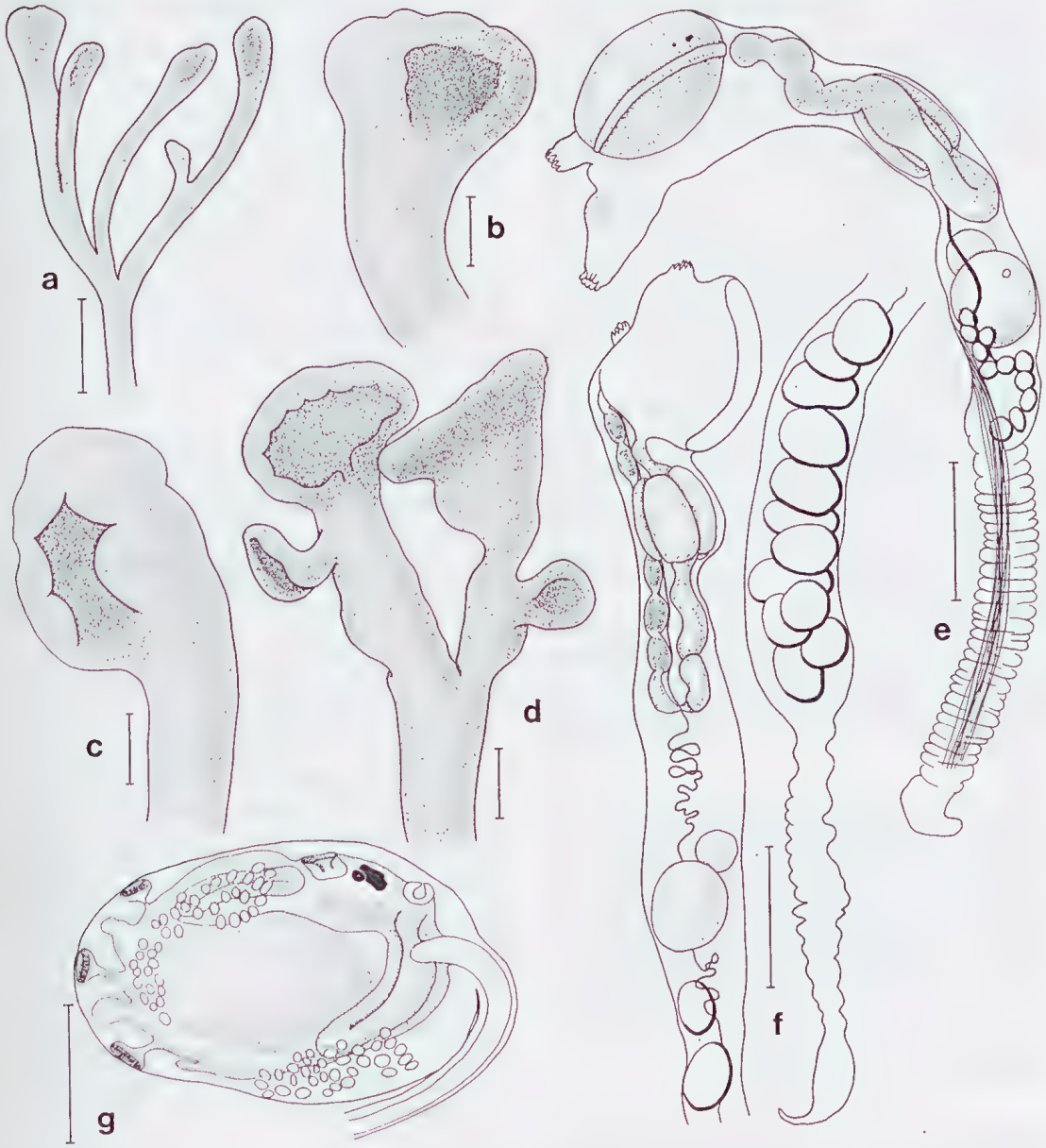


FIG. 10: *Ritterella pedunculata* — **a–d**, parts of colony and separate lobes (**a–c**, QM G9292; **d**, MV F57794); **e**, **f**, zooids (**e**, F57793; **f**, MV F57794); **g**, larva (MV F57793). Scales: **a**, 5mm; **b**, **c**, 1mm; **d**, 2mm; **e**, **f**, 0.5mm; **g**, 0.2mm.

basal stolons, and with flattened spatulate to fan-shaped tips which sometimes curve around to form a cornet, interrupted at one side. Up to 12 zooids are present in each lobe although usually there are fewer. The atrial openings are around the inside rim of the terminal, curved lamella and the branchial apertures around the outside of its rounded rim. Sand is thick externally but absent internally. Despite their outer layer of sand, collector's notes record specimens from St. Vincent Gulf (SAM E2450) to have been bright red.

INTERNAL STRUCTURE: The zooids are thread-like, the thorax and abdomen together up to 5mm long and with a much longer posterior abdomen. The apertures are almost sessile on short siphons, the rim of each with 8 small triangular lobes. Some fine circular muscle bands are on the thorax and the siphons. The longitudinal bands are delicate and extend the length of the zooid. There are 5 rows of about 12 stigmata. Neither parastigmatic vessels nor branchial papillae are present. Triangular dorsal languets are present over the dorsal sinus, on the transverse vessels.

The gut loop is slightly longer than the thorax, the oesophagus is short and the small stomach, smooth when distended but with 5 folds when collapsed, is not quite halfway down the abdomen. There is a distinct duodenal region and a posterior stomach in the descending limb of the gut loop. A rectal gland is at the junction of the mid-intestine and rectum.

The testis follicles are almost cylindrical, oriented longitudinally, and in a single series. When the posterior abdomen is contracted the male follicles are slightly bunched together. The small ovary is anterior to the testis, just behind the gut loop.

Up to 2 embryos, some developed to tailed larvae, are in the atrial cavity of specimens collected in February from Bruny I. (Tasmania) and Elliston Bay (S. Australia), in July from Portland (Victoria), and November (St. Vincent Gulf). The larval trunk is 0.6mm long. Single median ectodermal ampullae alternate with the adhesive organs. Ampullary vesicles are in bilateral clumps, about 3 deep postero-ventrally, antero-dorsally and around the anterior end of the trunk. Both otolith and ocellus are present.

REMARKS

Colonies from Green Pools (AM U3896, see below) assigned to this species by Kott (1957) are specimens of *Dumus*, having single zooids in each lobe, and 4 rows of stigmata.

Superficially, colonies of *R. pedunculata* resemble *R. cornuta*, *R. papillata*, and *R. asymmetrica* as well as *Monniotus* spp. and *Dumus* spp. However *Dumus* and *Monniotus* are distinguished by having only one zooid in each lobe; and the other *Ritterella* spp. have differently organised colonial systems, the shapes of the terminal free ends of each lobe being different (see *R. cornuta*, REMARKS). *Ritterella pedunculata* can also be distinguished from other *Ritterella* spp. by details of the branchial sac — from *R. asymmetrica* and *R. cornuta* by the 5 simple rows of stigmata, and from the latter and *R. papillata* by the absence of branchial papillae.

The specimens with both parastigmatic vessels and a branchial papillae on each transverse vessel reported from St. Vincent Gulf by Kott (1972a) are juveniles of *Monniotus australis*. There are neither branchial papillae nor parastigmatic vessels in *R. pedunculata*. Larvae from Elliston Bay (Kott 1975, Fig. 1) have a larval trunk 0.6mm long as do the newly recorded larvae from Bruny I. (MV F57793).

Genus **Dumus** Brewin, 1952

Type species: *Dumus areniferus* Brewin, 1952.

Only 2 species are known. Colonies are narrow, sandy, branched vertical lobes, the terminal branch containing only a single zooid, with 4 rows of stigmata, and a smooth or mulberry-like (but never folded) stomach wall. Possibly associated with the reduction in size of the branchial sac, there are no branchial papillae. Parastigmatic vessels sometimes are present. Testis follicles are in a single longitudinal series, relatively numerous eggs (to about 10) are present in the ovary and up to 12 embryos at a time are incubated in the atrial cavity. Many species of *Ritterella* (e.g. *R. pedunculata*) have similar colonies but otherwise are separated from *Dumus* by their more numerous rows of branchial stigmata, embedded zooids and longitudinal stomach ridges.

Nevertheless, the relatively large numbers of eggs in the ovary and the number of embryos incubated in *Dumus* suggest a more primitive condition than in *Ritterella* (in which not more than 3 embryos at a time are incubated in the atrial cavity).

The only species known are the type from New Zealand and temperate Australian waters, its northern limit in Moreton Bay), and *Dumus dumosus* (Monniot, 1987) from New Caledonia, a species originally assigned to the genus *Euherd-*

mania. It has neither the long oesophagus nor the folded stomach wall, nor the characteristic larval adhesive organs of *Euherdmania*. Its colonies are similar to those of *D. areniferus*, from which it differs in the presence of scattered circular swellings in the stomach wall and the parastigmatic vessels (as in *R. arenosa*, *R. asymmetrica*, *R. tokioka*, *R. yamazii*, and occasionally in *Condominium areolatum*, see above).

Dumus areniferus Brewin, 1952
(Fig. 11)

Dumus areniferus Brewin, 1952, p. 453. Kott, 1976, p. 58. Millar, 1982, p. 43.
Ritterella herdmania Kott, 1957, p. 102 (part, specimens from Green Pools).

DISTRIBUTION
NEW RECORDS: South Australia (Price I., QM GH4152). Victoria (Portland, QM GH92). New South Wales (South Ulladulla, QM G8585). Queensland (Moreton Bay QM G12725 GH3901 GH3903 GH4247).
PREVIOUSLY RECORDED: Western Australia (Green Pools — AM U3896). Victoria (Westernport — MV H286 QM G7509, AM Y1980 Kott 1976). New Zealand (Otago — Brewin 1952).

The range of this species, in Queensland and New Zealand, suggests a Gondwana component of the fauna.

DESCRIPTION
EXTERNAL APPEARANCE: Colonies are aggregations of long, narrow, sandy, branching vertical stalks up to 6cm long, joined to basal common stolons. The vertical stalks adhere to one another by the sand that covers them to form sandy platforms. The free ends of each terminal branch are expanded into a short bulb bent ventrally at right angles to the long axis of the stalk, onto which the zooids open. A single zooid is in each terminal branch of the colony. The branchial apertures face downwards from the front of the bulb and the atrial aperture upwards from the top. The thorax is slightly flattened dorso-ventrally. The stalks all taper slightly toward the base.

INTERNAL STRUCTURE: Zooids are up to 6mm long, and thread-like, at least half of the length being posterior abdomen. Six sharply pointed lobes surround each aperture. The body wall is muscular with 10 external longitudinal bands extending obliquely across the thorax from the branchial siphon to the postero-dorsal corner and then along the whole length of the zooid. From 10 to 16 stigmata are in each of 4 rows. Neither branchial papillae nor parastigmatic vessels are present. The smooth-walled almost cylindrical stomach occupies the middle third of the abdomen. The anal opening is halfway up the thorax. The ovary in the anterior part of the posterior abdomen has up to 10 eggs. Long and oval or, when compressed by contraction, circular to pear-shaped testis follicles are in a single series, although with contraction they tend to become bunched. Kott (1976) reported testis follicles confined to the posterior half of the posterior abdomen, but in the newly recorded specimens from South Australia and Queensland they occupy its whole length.

Up to 12 embryos are crowded in the atrial cavity of specimens collected in July (QM G8586) and August (QM GH3901 GH4247) from Moreton Bay, and November (AM Y3896 Y1980) from Green Pools and Westernport. The larval trunk is 0.4 to 0.5mm long. The 3 adhesive organs have narrow stalks and small, shallow cones of secretory cells. They alternate with median ampullae, each of which has a lateral ampulla near its base. On each side, there also are clumps of postero-ventral and antero-dorsal ampullary vesicles, the latter extending around the anterior end of the trunk, outside the lateral ampullae. The tail is wound about two-thirds of the way around the trunk. An otolith and ocellus are in the cerebral vesicle. The adhesive organs in this species are particularly small, and the robust ectodermal ampullae appear to be the most important structures at the anterior end of the trunk, and they have a cap of enlarged epidermal cells similar to those in *Polyclinum*.

REMARKS
The great geographic range of this species is not reflected in a variable morphology, for there is little variation, even between Australian and New Zealand populations. Although the larva is smaller, and lacks the lateral ampullae, it generally resembles the larva of *Ritterella pedunculata*.

Family EUHERDMANIIDAE Ritter, 1904
emend.

Zooids are either separate or embedded, with 6-lobed atrial openings directly to the surface. A long oesophagus opens into a small, longitudinally ridged stomach at the posterior end of the abdomen. The wide rows of stigmata (50 to 100 per row) vary in number from 5 to 20. Neither

parastigmatic vessels nor branchial papillae are present. The anus opens in the base of the atrial cavity. Gonads are bunched, in a relatively short abdomen. Fertilisation takes place at the proximal end of the oviduct and embryos are brooded in the oviduct. Larvae have long pycnoclavellid-type inverted tubular adhesive organs.

Usually longitudinal and oblique muscles from the branchial and atrial siphons cross the thoracic wall to join into a wide band along each side of the ventral border, and continue onto the abdomen and posterior abdomen in 2 wide bands. In *E. vitrea* Millar, 1961 a dorsal rather than ventral band of muscles is reported and in *E. morgani*

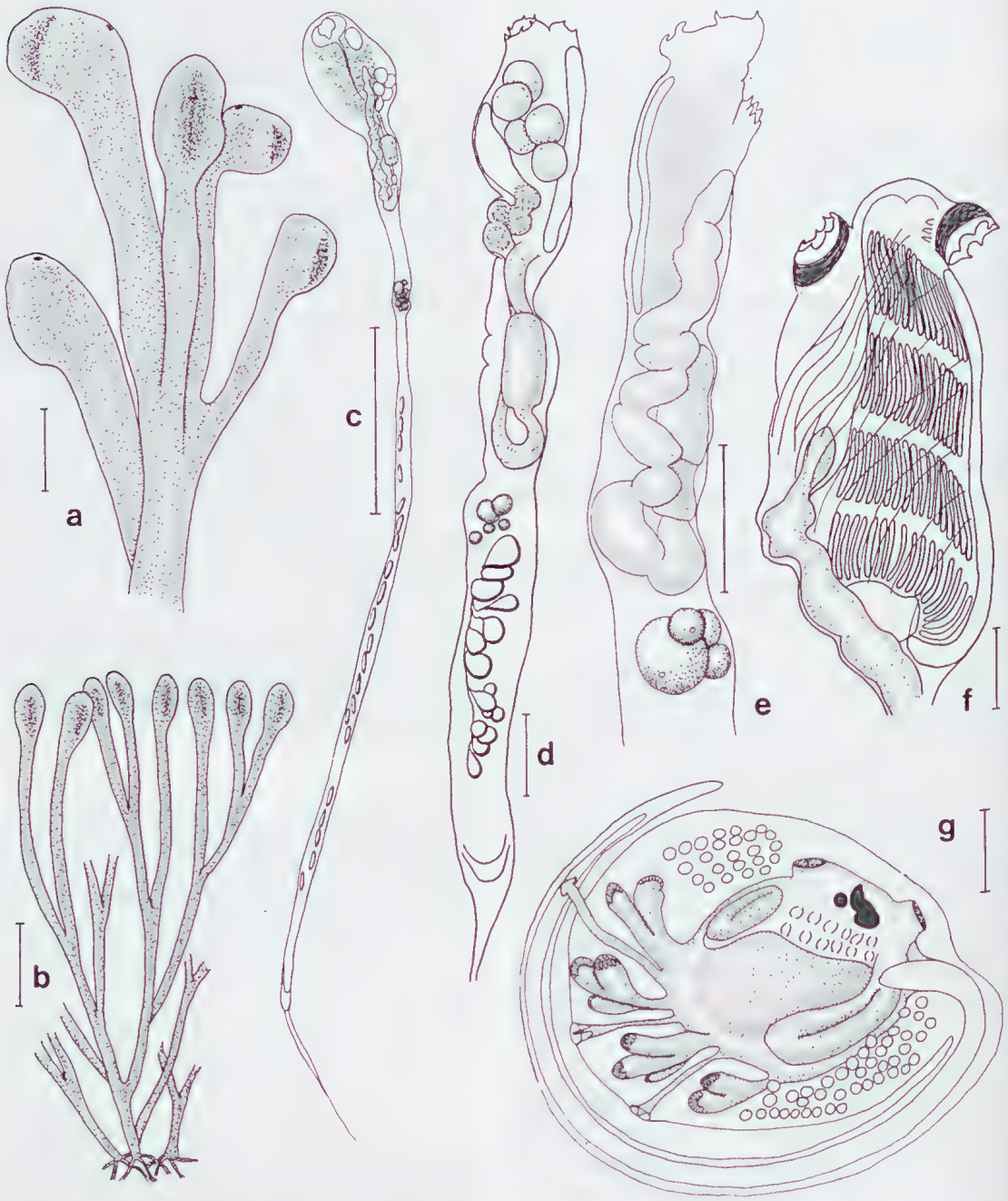


FIG. 11: *Dumus areniferus* — **a**, **b**, parts of colonies (**a**, QM GH4152; **b**, QM GH3901); **c–f**, zooids and parts of zooids (QM GH3901); **g**, larva (AM Y1980). Scales: **a**, 2mm; **b**, **c**, 5mm; **d–f**, 0.5mm; **g**, 0.1mm.

Millar and Goodbody, 1974 both ventral and dorsal bands are present. Transverse muscles have been reported only for *E. fasciculata* Monniot, 1983.

Pycnoclavellidae (see Kott 1990, p.66) have the same range in colony form as the present family, having zooids completely or partially embedded, or separate from one another for most of their length. Pycnoclavellidae also resemble the species of the present family in the position of the anal opening, the long oesophagus, fertilisation at the base of the oviduct and the same type of larval adhesive organs.

The principal characters distinguishing Euherdmaniidae from Pycnoclavellidae are the 6-lobed (rather than smooth) apertures, and the relatively large gonads sometimes located in a posterior abdomen (rather than in the gut loop). The relationship between the families seems to be closer than either has with other families.

Euherdmania is the only known genus of the family Euherdmaniidae.

When a posterior abdomen is not present (*Euherdmania dentatosiphonis*, *E. digitata* and *E. translucida* n.sp.), difficulties can arise in separating certain species of *Euherdmania* from *Polycitor*. Both have a long oesophagus and lobed apertures. The presence of larvae can resolve the difficulty as those of *Euherdmania* have long, inverted tubular (pycnoclavellid-type) adhesive organs. In the absence of larvae, reliance must be placed on the width of the thorax, position of the anal opening, and other details of the siphonal lobes to separate the genera.

Genus **Euherdmania** (Ritter, 1904)

Type species: *Euherdmania claviformis* (Ritter, 1903).

The genus is characterised by its separately opening zooids with long oesophagus and folded stomach wall.

In addition to the new species described below, the known species of *Euherdmania* are:

Euherdmania gigantea (Van Name, 1921) from Florida has embedded zooids and conspicuously serrated lobes around the apertures. Kott (1981) argued that the denticulate lobes of the apertures may indicate synonymy with *Stomozoa*. However, this is denied by the position of the gonads and the presence, in *E. gigantea*, of a series of embryos in the abdominal part of the oviduct (see Millar 1977) — as in *Euherdmania* but not in *Stomozoa*. The serrated lobes around the apertures probably occur in parallel in these taxa. Millar (1977) re-examined the holotype of *E. vitrea* Millar, 1961 from the Brazilian coast and thought that it may be conspecific with *E. gigantea*. A doubt remains, however, since the holotype zooids described (Millar 1961) have a dorsal rather than the ventral muscle bundle present in *E. gigantea*.

Euherdmania dentatosiphonis (Millar, 1975) from the western Pacific, was thought to be a synonym of *E. digitata* (see Kott 1981). However, it differs from *E. digitata* in having similar serrated lobes around the apertures to those in *E. gigantea*.

Euherdmania morgani Millar and Goodbody, 1974 differs from *E. gigantea* in its shallow and smooth (rather than serrated) oral and atrial lobes, its dorsal, as well as ventral, thoracic muscles, and zooids opening around a stalked, fan-shaped head rather than on top of a thick, sessile upright colony.

Euherdmania digitata Millar, 1963 from north-western Australia and the Western Pacific (Kott 1981, Tokioka 1967, Nishikawa 1984a) and southern Australia (see below) has separate zooids joined by basal stolons or common test. Occasionally its gonads are in the gut loop rather than in a posterior abdomen. It differs from *E. claviformis* in that the test is not sand-covered and the lobes of the colony are thicker. The larvae have the characteristic inverted tubular adhesive organs.

Euherdmania solida Millar, 1953 from the Gold Coast (Ghana) differs from *E. digitata* only in having partially embedded zooids. Its body musculature is like that of *E. digitata* and *E. vitrea*.

Euherdmania rodei Pérès, 1949 from the Gold Coast (Ghana) has fewer stomach folds than *E. solida* and completely embedded zooids.

Euherdmania claviformis (Ritter, 1903) from California has, like *Monniotus* spp. long, narrow, sandy lobes, each containing a single zooid, united basally. It is distinguished from zooids of the latter genus by the long oesophagus characteristic of *Euherdmania*. A related species from Senegal, *E. claviformis*: Pérès, 1949 has 15 to 16 rows of stigmata rather than 8 to 12 found in the Californian species. *Euherdmania claviformis*: Monniot, 1987 from New Caledonia with 18 rows of 40 stigmata is wrongly assigned (see *E. digitata* below).

Euherdmania fasciculata Monniot, 1983 from Guadaloupe has long, narrow branching stalks with the thoraces, at least, separate from one another. Sand is present only on the base of the colony. Longitudinal and transverse muscles form a meshwork and the

longitudinal ones go to the end of the posterior abdomen. There are 12 to 17 rows of up to 30 stigmata. The anterior row of stigmata curves anteriorly along dorsal line. The anus opens at the second-last row of stigmata. The oesophagus is long, and the stomach is in the posterior end of the long abdomen. The species is separated from *E. claviformis* by its more numerous stomach folds (10 rather than 6), and its naked test.

Euherdmania areolata Millar, 1978 from the western Atlantic (Guyana shelf), has long, narrow, sandy lobes, each of the terminal branches containing a single zooid. These colonies resemble *E. claviformis* but they have more branches. The stomach has internal folds which are not obvious externally and distinguish the species from *E. claviformis* and *E. fasciculata*.

Thus, there appear to be 3 groups of species in *Euherdmania*, viz.:

a.*Gigantea* group with separate or embedded zooids, and pronounced serrations on siphonal lobes (*E. gigantea*, *E. dentatosiphonis*, *E. translucida* n.sp. and possibly *E. vitrea*).

b.*Digitata* group with separate or embedded (partially or completely) zooids, gelatinous sand-free test, and shallow, smooth siphonal lobes (*E. digitata*, *E. solida*, *E. rodei*, and probably *E. morgani*). *Distoma pulchra* Ritter, 1901 (<*Sigillinaria pulchra*: Van Name, 1945) is a likely member of this group.

c.*Claviformis* group with separate zooids in long, narrow, sometimes sandy, sometimes branching stalks, and pronounced but not serrated siphonal lobes (*E. claviformis*, *E. areolata* and *E. fasciculata*). The colonies of this group of species resemble those of many Ritterellidae, and *Monniotus* spp.

Larvae are known for *E. vitrea* (see Millar, 1961), *E. claviformis* (see Trason 1957); *E. digitata* (see Millar 1963, Kott 1981 and below). The larvae of *E. gigantea*, *E. rodei*, *E. dentatosiphonis*, *E. translucida* n.sp., *E. areolata* and *E. solida* are not known.

Euherdmania australis Kott, 1963 is incorrectly assigned having a short oesophagus, branchial papillae on the transverse branchial vessels, parastigmatic vessels, a stomach wall areolated but not longitudinally ridged, and a polyclinid-like larva with ectodermal ampullae and vesicles, and stalked adhesive organs (see *Monniotus*). *Euherdmania dumosa* Monniot, 1987 is also incorrectly assigned (see *Dumus*).

Species of *Euherdmania* are known mainly from tropical oceans and generally they have relatively restricted ranges. *Euherdmania translucida* n.sp. from South Australia related to *E. dentatosiphonis*, and the eastern Pacific *E. claviformis* are the only records from temperate waters.

Key to species of *Euherdmania* recorded from Australia

1. Siphonal lobes serrated 2
   Siphonal lobes not serrated ..... *E. digitata*
2. Thoracic muscles not more than 3; colonial .... *E. dentatosiphonis*
   Thoracic muscles more than 3; solitary .... *E. translucida* n.sp.

Euherdmania dentatosiphonis (Millar, 1975) (Fig. 12)

Clavelina dentatosiphonis Millar, 1975, p. 211.

DISTRIBUTION

NEW RECORDS: None.

PREVIOUSLY RECORDED: Queensland (Coral Sea, Millar 1975).

The single small colony was taken at 100m.

DESCRIPTION (after Millar 1975)

EXTERNAL APPEARANCE: The single small colony consists of 4 narrow-stalked, club-shaped lobes attached to a basal stolon. Each lobe contains a single zooid, although in 2 they are degenerate or developing. The largest lobe is about 2cm high. The test is gelatinous and translucent, the thoracic part delicate and the stalk rather firm. The branchial aperture is terminal, but turned ventrally, and the atrial aperture is on the dorsal surface. Zooids are pink in preservative and can be seen through the test.

INTERNAL STRUCTURE: The larger zooid is 6mm when removed from the test. Each of the 6 lobes of each aperture is denticulate. The anterior lobe of the atrial aperture and the dorsal lobe of the branchial are broad. There is a half velum inside the 5 smaller lobes of each aperture which partly occludes the opening. The branchial tentacles, numbering about 45 are on the edge of a velum at the base of the branchial siphon. There are 3 wide oblique muscle bands on each side of the thorax, extending from the base of the atrial siphon to the postero-ventral corner of the thorax. These join into a single band running along the

ventral surface of the abdomen, one on each side of the mid-line. Millar (1975) found 16 rows of stigmata alternating with high transverse branchial vessels. Triangular, pointed dorsal languets are present on the dorsal sinus. The abdomen of Millar's specimen may have been mutilated, as there was no sign of either stomach or gonads, although there is an entire gut loop.

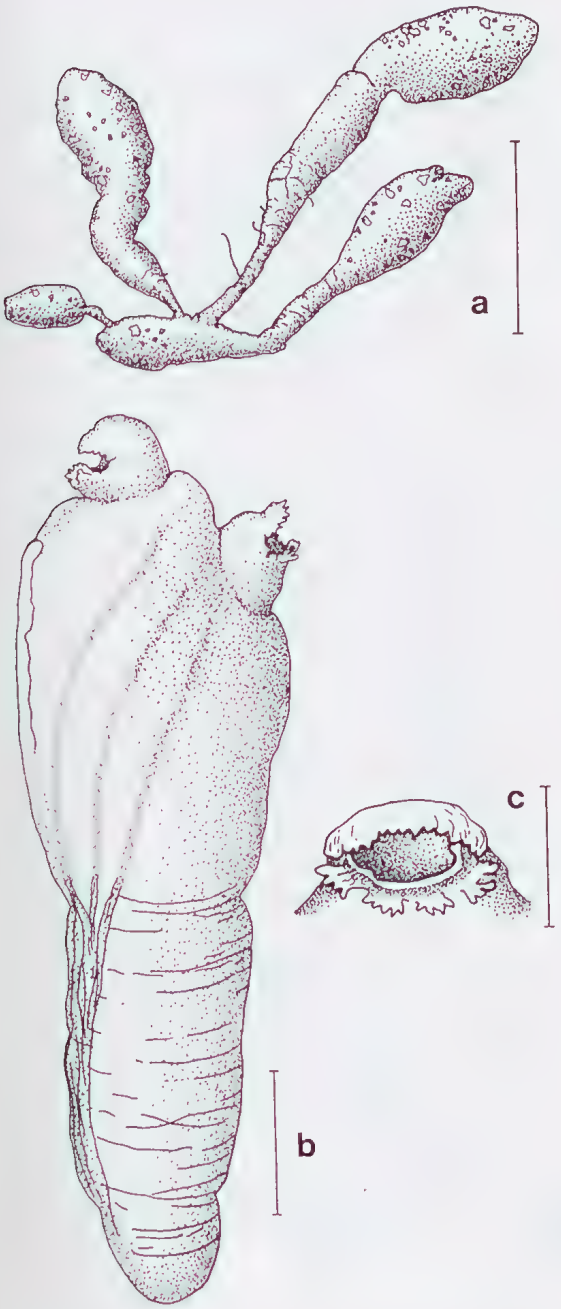


FIG. 12: *Euherdmania dentatosiphonis* (after Millar 1977) — **a**, part of colony; **b**, zooid contracted; **c**, lobes of branchial aperture. Scales: **a**, 1cm; **b**, **c**, 1mm.

REMARKS

Kott (1981) believed that this species was a junior synonym of *Euherdmania digitata* Millar, 1963, which is known from the Western Pacific (Tokioka 1967, Kott 1981), north western Australia (Millar 1963) and southern Australia (see below). However, as well as lacking the denticulate lobes of the present species, *E. digitata* differs in the arrangement of its body muscles, including the presence of transverse thoracic muscles. The present species has similar siphonal lobes to *Euherdmania translucida* n.sp. from southern Australia. However, *E. translucida* has a larger zooid, more numerous thoracic muscles, and a solitary habit, all of which distinguishes it from *E. dentatosiphonis*. Further, the different locations in which they have been found and the discontinuity in their ranges is a compelling argument in favour of separate species.

Euherdmania gigantea (Van Name, 1921), from the western Atlantic (see Millar, 1977), has similar denticulate lobes and half velum in the aperture. It differs from the present species mainly in the form of the colony with its embedded zooids, and its more numerous oblique thoracic muscles (joining the usual bands each side of the mid-ventral line).

Millar (1975) thought that the upper part of the corrugated tube in the abdomen of the type specimen of *E. dentatosiphonis* may be the stomach, and Kott (1981) thought that the presence of a stomach at more or less the same level in the abdomen of *Euherdmania digitata* confirmed Millar's view. However it seems more likely that the abdomen of the type of *E. dentatosiphonis* has been damaged, and that it will be found to have a longitudinally folded stomach in the posterior part of the abdomen, as in all known *Euherdmania* spp., including species such as *E. translucida* n.sp. and *E. gigantea* which have other characters in common.

Euherdmania digitata Millar, 1963
(Fig. 13. Plate 2e)

Euherdmania digitata Millar, 1963, p. 698. Tokioka, 1967, p. 58. Kott, 1981, p. 154. Nishikawa, 1984a, p. 113. Monniot and Monniot, 1987, p. 83.
Euherdmania claviformis: Monniot, 1987, p. 501.

DISTRIBUTION

NEW RECORDS: South Australia (Investigator Group, QM GH4920 GH4183). Queensland (Capricorn Group, QM GH2455 GH4919 GH4921–5; Lizard I., QM G9772 GH2442).

PREVIOUSLY RECORDED: Western Australia (Cape Boileau — Millar 1963). New Caledonia (Monniot 1987). Fiji (QM G12469–70 G12867–8 Kott 1981). Palau Is (Tokioka 1967). Ponape (Nishikawa 1984a). Moorea, Tahiti (Monniot and Monniot 1987).

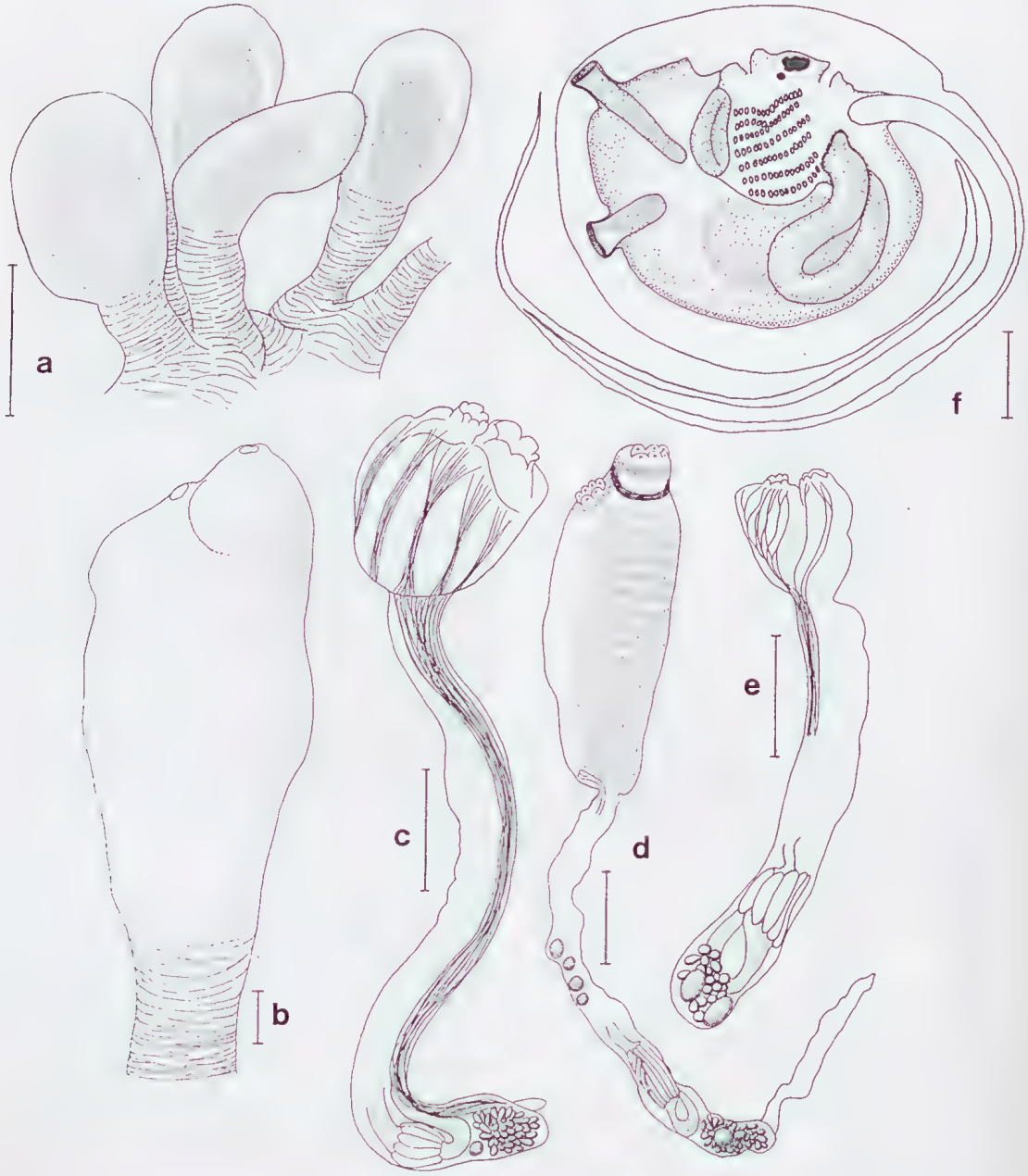


FIG. 13: *Euherdmania digitata* — **a**, part of colony (QM GH4920); **b**, single zooid in test (QM GH4183); **c–e**, zooids at various states of contraction (**c**, **d**, QM GH4920; **e**, QM GH4183); **f**, larva (QM G9772). Scales: **a**, 5mm; **b**, 1mm; **c–e**, 2mm; **f**, 0.2mm).

Description

EXTERNAL APPEARANCE: Colonies are up to 4cm in maximum extent, consisting of separate zooids up to 3cm high attached to a tangle of basal stolons or solid basal test. The lower one-third of each upright zooid is covered with very firm test, which becomes progressively softer and more transparent toward the upper (thoracic) part. The upright stalks sometimes branch along their length.

The thoracic test has a thickening each side of the terminal branchial aperture and another median one just postero-dorsal to the subterminal atrial opening.

The living specimens from the Capricorn Group are a clear, bright canary-yellow, and one of the zooids (from QM GH4925) had *Prochloron* symbionts evenly and densely distributed around, and in the lining of, the branchial siphon. Yellow pigment is especially dense in both siphon linings.

The rim of each of the apertures is divided into 6 shallow lobes, each lobe with a yellow (light sensitive ocellus?) pigment spot in the centre. The branchial aperture often is inclined ventrally, and the atrial aperture directed upwards.

INTERNAL STRUCTURE: Zooids are long (up to 3cm) and narrow. The thorax is about a quarter of the length of the abdomen. The posterior abdomen, only slightly shorter than the abdomen, terminates in several blunt vascular processes. Up to 20 fine parallel longitudinal thoracic muscles, which when contracted form 8 to 10 wide bands, cross the thorax obliquely from atrial and branchial apertures to the endostyle, and continue along each side of the mid-line on the abdomen and posterior abdomen in a pair of wide ventral bands. A layer of fine transverse muscles lies beneath the longitudinal muscles on the thorax. About 20 very slender branchial tentacles are in a circle at the base of the branchial siphon. About 16 to 18 rows of stigmata have approximately 50 to 60 stigmata per row in the anterior rows. Shorter rows with about 30 stigmata are at the posterior end of the branchial sac. Transverse vessels are broad, flat membranes projecting between the rows of stigmata. These expand into long, pointed dorsal languets over the dorsal sinus.

The gut loop is long and narrow, with a long oesophagus and a narrow stomach at the posterior end of the descending limb. The stomach wall has from 8 to 12 longitudinal irregular, or oblique and sometimes shallow folds. The anal opening has two smooth lips and opens in the base of the atrial cavity.

Gonads are in the anterior part of the posterior abdomen, just behind the stomach. They consist of a cluster of pyriform male follicles, surrounding 3 or 4 oocytes. In one of the specimens there are also orange eggs in the oviduct and in others a developmental series of embryos is in the oviduct from just distal to the stomach to the atrial cavity. Embryos are present in the oviduct in June from Lizard I. (QM G9772), but were not present in October at Heron I. Larvae have a long (1.0mm) trunk, with 2 long inverted tubular adhesive organs, an ocellus and an otolith. The tail is wound about halfway around the trunk. The postero-ventral part of the trunk is very yolky.

Remarks

The zooids and larvae of the north-western Australian (Millar 1963), and Palau Is (Tokioka 1967) specimens deviate from the present ones only to the extent that a lesser number of stigmata (15) was recorded for the Palau Is specimen. However, Tokioka was uncertain about the numbers he recorded and it is possible that he was misled by the narrow thorax.

Monniot (1987) assigned New Caledonian colonies (an unspecified number) to the indigenous Californian *E. claviformis*, which has fewer rows of stigmata and narrower thoraces. There is neither morphological nor geographic grounds for this assignation. Larvae are the same size as the other western Pacific specimens. It is presumed that the 2 adhesive organs recorded by Monniot are the usual inverted tubes characteristic of this genus.

Kott (1981) tried to establish a synonymy between the present species and *E. dentatosiphonis* Millar, 1975. She thought the denticulate siphonal lobes of *E. dentatosiphonis* were not essentially different from the smooth lobes of the Fijian specimens of *E. digitata*. However, comparison of the Fijian with the newly recorded Australian specimens shows them to be similar to one another, and distinct from *E. dentatosiphonis*. The larvae and embryos being incubated in the oviduct of Fijian and Australian specimens are also identical; and re-examination of the Fijian specimens has shown that although only 20 stigmata were recorded, at least twice that number is present.

Of concern to the interpretation of intrageneric phylogeny of these taxa is the variation in the position of the gonads, which are in the abdomen (in the Fijian specimens), or in a posterior abdo-

men. However, although the former have embryos in the oviduct, and tubular larval adhesive organs like *Pycnoclavella*, their siphonal lobes indicate that the specimens are members of the genus *Euherdmania*, and in view of their other characters, they appear to be specimens of *E. digitata*.

Variation in the number, orientation and depth of the stomach folds apparently is a characteristic of this species, Millar (1963) and Kott (1981) reporting 12 folds, Tokioka (1967) reporting 8, and Monniot (1987) 6 to 10 but mostly 8.

Euherdmania translucida n.sp.
(Fig. 14. Plate 3a)

DISTRIBUTION

TYPE LOCALITY: South Australia (Sir Joseph Banks Group, Marum I., N Point, offshore, in sand and root-mat of *Posidonia*, 8m, coll. W. Zeidler 11.1.84, holotype SAM E2092, paratype SAM E2056; Sir Joseph Banks Group, Reevesby I., NW Point 150–200m, coll. W. Zeidler, paratype SAM E2093).

FURTHER RECORDS: South Australia (Spencer Gulf, Banks and Investigator Groups, QM GH2310, SAM E2091; Yorke Peninsula, SAM E2455; Kangaroo I., SAM E2529).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are solitary, up to 4cm high. They have hard, long, narrow stalks with basal branching root-like extensions. Only 3 specimens (SAM E2056 E2092 E2455) are complete. The others have been cut off across the long oesphageal neck and the posterior end of the abdomen is missing. The base of the stalks of the holotype and one paratype (SAM E2056) expand into a holdfast amongst the *Posidonia* root mat. The firm stalk has whitish, translucent test internally, and is leathery externally. The terminal expanded balloon-shaped thoracic part, occupying about one-fifth of the total length, has thick, soft, and glassy test containing spherical test cells which are crowded together forming spots about 0.5mm apart. The branchial aperture is terminal and the atrial aperture subterminal. Each aperture is surrounded by 6 large, rounded petal-like lobes.

Photographs of living specimens show them to have very transparent thoraces, with bright spots which may be light sensitive at the tips of the siphonal lobes.

INTERNAL STRUCTURE: The zooid occupies the whole length of the stalk, with only a fine blood vessel extending into the basal holdfast.

Each aperture is surrounded by 6 flat lobes. A crescent-shaped half velum is around the ventral side of the lumen of the branchial aperture, and another is inside the dorsal side of the atrial aperture. The adjacent lobes of the respective apertures, viz., the dorsal lobe of the branchial and the ventral (or anterior) lobe of the atrial aperture are especially wide, each containing parallel longitudinal muscles and fringed with about 12 pointed tongues. The inner faces of these 2 large, fringed lobes are continuous with the lining of the pharyngeal and atrial cavities respectively. Continuity between the linings of these cavities and the inside surfaces of the slightly smaller lateral lobes (fringed with 6 to 8 points) on each side of the large median lobes is interrupted by the ends of the crescent-shaped vela. Outside the widest part of the vela, the tip of the opposite median and lateral lobes are divided into one or 2 long points.

A sphincter muscle in each velum seems to derive its fibres from the longitudinal thoracic muscles. Seen in section, the velum appears to be a fold of the body wall at the base of the siphons. The branchial velum in particular projects from just in front of the branchial tentacles, and its sphincter muscle may be homologous with that usually found beneath the tentacles. There are 12 strong longitudinal thoracic muscles, viz. 4 branchial contributing fibres to the branchial velum, 3 dorsal contributing fibres to the 2 large median siphonal lobes, and 3 atrial contributing fibres to the atrial velum. These muscles extend obliquely toward the postero-ventral corner of the thorax, and join into a wide band on each side of the long oesophageal neck, terminating at the posterior end of the abdomen. Transverse muscles were not detected.

About 40 relatively long, slender branchial tentacles are of various sizes. The dorsal gland is large, and a fleshy dorsal tubercle has a vertical opening in a V-shaped peritubercular area that projects into the pharynx so that the opening of the neural duct is directed forwards, toward the branchial aperture. There are 20 long rows of relatively short stigmata, with 100 or more stigmata in the anterior rows, although the rows become shorter posteriorly. The transverse vessels between the rows of stigmata are very wide, flat membranes. Over the dorsal sinus these expand into triangular languets with long points that coil over to the right side. Neither parastigmatic vessels, nor papillae are on the transverse vessels.

The oesophageal neck is long and straight, and the abdomen swells into an onion-shaped bulb

only at the posterior end. Both the oesophagus and rectum are transversely wrinkled. In the only 2 specimens with a complete abdomen, the stomach, and other parts of the gut loop, have very thin walls and are packed with trophocyte cells. The abdomen appears to be degenerating and possibly the body organs are being resorbed. The stomach is almost cylindrical with about 6 longitudinal folds. There is no apparent posterior abdomen. The pole of the gut loop curves around in the posterior end of the abdomen. The anal opening is at the posterior end of the atrial cavity. There were no gonads detected in these specimens; nor were larvae present.

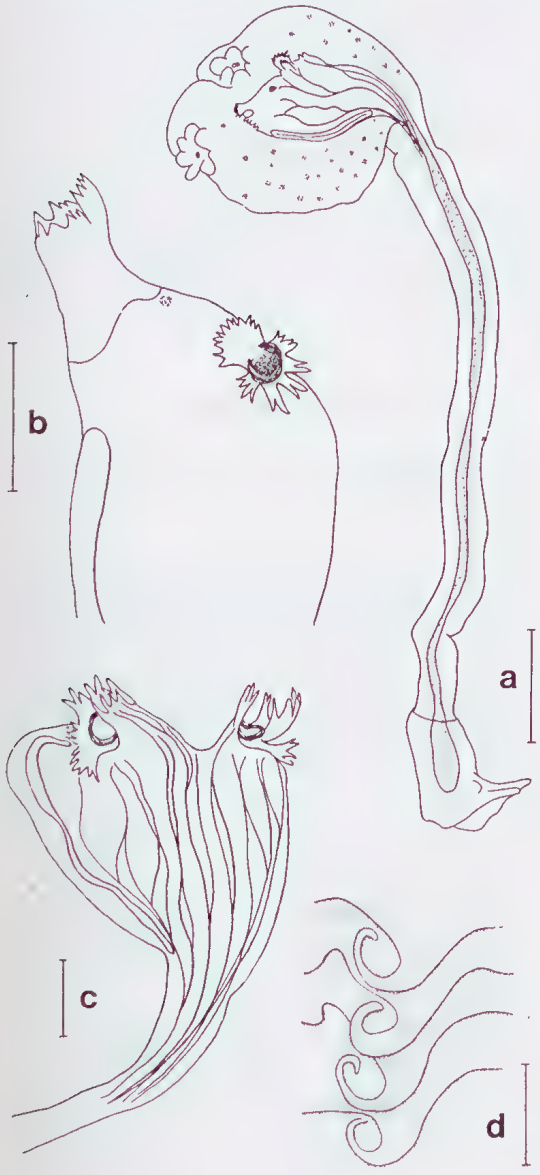


FIG. 14: *Euherdmania translucida* n.sp. — **a**, zooid in test (holotype SAM E2092); **b**, **c**, thoraces showing lobes of apertures and muscles (SAM E2093 E2091); **d**, part of dorsal lamina (SAM E2091). Scales: **a**, 5mm; **b**, **c**, 2mm; **d**, 0.5mm.

REMARKS

A number of characters can cause confusion in identifying this species. There are certain solitary *Clavelina* (e.g. *C. meridionalis*, *C. ostrearium*, *C. dagysa*) that superficially resemble the solitary individuals of *E. translucida*, but they have a characteristically conspicuous vascular stolon and plain-rimmed apertures (the present species has only a small inconspicuous vascular stolon and lobed apertures). The size of the pharynx, the number of stigmata as well as the number of rows, the absence of a posterior abdomen and the large siphonal lobes suggest *Stomozoa* but, in addition to their colonial habit, *Stomozoa* spp. have complete rather than partial siphonal vela, the so-called ocelli are on each side of the siphonal lobes rather than in the tips as they are in the present species, and the oesophagus is not as long as it is in the present species.

The long abdomen, long oesophagus and anus in the posterior end of the atrial cavity are characteristic of both *Pycnoclavella* and *Euherdmania*. Nevertheless, the species seems closer to *Euherdmania* than *Pycnoclavella* because of its large pharynx with numerous rows of stigmata, folded stomach, siphonal lobes, and muscular velum (which resembles that of *Euherdmania dentatosiphonis* Millar, 1975). Only its solitary habit, larger zooids and more numerous thoracic muscles distinguish the present species from *E. dentatosiphonis*. Thus, although the gonads are not always in a posterior abdomen, *Euherdmania* seems to be the most appropriate genus for this species.

Family PSEUDODISTOMIDAE n. fam.

The family is characterised by its colonies with embedded, separately opening zooids with 6 well defined lobes around the atrial and the branchial apertures, 3 rows of stigmata with the anterior row on each side continuing anteriorly along each side of the mid-dorsal line, fertilisation in the oviduct, and a generally smooth stomach wall with 4 broad longitudinal compartments or quadrilateral in outline. Generally the oesophagus is short and the stomach is in the middle third of the abdomen.

However, a group of species, viz. *P. arborescens*, *P. aureum*, *P. novaezelandiae*, *P. opacum* and *Anadistoma* n.gen. (see below) have a longer oesophagus, with the stomach two-thirds to three-quarters of the distance down the abdomen. The curved heart is in the posterior tip of the posterior abdomen. Gonads are in longitudinal series or bunched in the long posterior abdomen. The vascular processes from the tip of the posterior abdomen are moderately long (longer than those in the Polycitoridae) and longitudinal muscle fibres (from the muscle bands on each side of the abdomen) sometimes continue onto them. Larvae are large, with a trunk often exceeding 1.0mm in length. The adhesive organs are large, with a deep, wide, eversible axial platforms which, when everted, form large thin-walled balloon-like structures in the anterior mid-line. They appear to lack the tall columnar cells that comprise the axial elements of the adhesive organs of most taxa (see Cloney 1977, Turon 1991).

Apart from the presence of gonads in a posterior abdomen, zooids resemble those of *Sigillina* in having 3 rows of stigmata, a relatively short oesophagus, smooth stomach, a long vascular stolon sometimes with longitudinal muscle fibres on it, fertilisation and incubation of the especially large embryos in the oviduct or in a brood pouch, and wide platforms of adhesive cells in the deep epidermal cups of the large, eversible adhesive organs. Further, in *Anadistoma* n.gen. transverse muscles are present on the thorax as in *Sigillina*.

Zooids are smaller than those of *Sigillina*, and, like those of *Eudistoma* and *Pycnoclavella*, have the anterior row of stigmata deflected anteriorly. This could be the result of convergent evolution associated with size reduction and does not necessarily indicate a direct relationship with Pycnoclavellidae. Nevertheless an alternative hypothesis for the origin of the Pseudodistomidae is from a pycnoclavellid ancestor by shortening of the gut loop, leaving gonads and heart in the posterior abdomen, while the tubular larval adhesive organs reduce in length and partially evert. Evidence against the pycnoclavellid relationship is the position of the anus halfway up the short thorax (not at the posterior end of the atrial cavity as in *Pycnoclavella*), and the 6-lobed rather than smooth apertures.

The monotypic genus *Citorclinum* Monniot and Millar, 1988, containing a single species *Citorclinum laboutei* Monniot and Millar, 1988 known only from the New Caledonian lagoon, appears to belong to this family. It has 3 rows of stigmata, the anterior row inclined forward along the mid-dorsal line, a smooth-walled stomach halfway down the abdomen, and the testis follicles in a long series in the posterior end of the posterior abdomen. As in *Pseudodistoma* incubation is in the abdominal part of the oviduct. The large larva (trunk about 1mm long) has 2 elongate everting adhesive organs in the mid-line. These are hollow, without columnar cells, and are like those of *Pseudodistoma* rather than *Sigillina*, or other Holozoidae, Polycitoridae and most families of the Aplousobranchia. The genus is distinguished from *Pseudodistoma* by the withdrawal of the heart and ovary to the abdomen with the gut loop, leaving the testes in the posterior abdomen.

In addition to *Citorclinum* and *Pseudodistoma* the family contains the monotypic new genus *Anadistoma*. The latter has transverse thoracic muscles and a longer oesophagus than *Pseudodistoma*.

Genus **Pseudodistoma** Michaelsen, 1924

Type species: *Pseudodistoma cereum* Michaelsen, 1924

Brewin (1958) on the basis of what she called 'parallelism in classification' assigned species to genera solely on the presence or absence of stomach folds — those with stomach folds being in *Pseudodistoma*. This definition is based on the type species which has a quadrate stomach or one partially divided into 4 chambers. True stomach folds do not occur. Brewin's definition must also be amended to exclude *Ritterella* in which true stomach folds do occur, and which has other characters separating it from *Pseudodistoma*.

Species of this genus appear to be less prolific than most ascidians. Gonads apparently mature for only a short time, and were not seen in many of the examined specimens. Further, the ovaries are small, and in most species only a single ovum develops at a time. The testis follicles are confined to the posterior, middle, or anterior part of the posterior abdomen, and never occupy its full length. Fertilisation appears to be at the base of the oviduct, for embryos are found being incubated in the posterior abdomen in *P. oriens* n.sp. and *P. kanako*; and in the abdomen in *P. arborescens*, *P. aureum*, *P. opacum*, *P. cereum*, and *P. brieni*. In the last 2 species embryos are lined up in the abdominal part of the oviduct in a developmental sequence. In the new Australian species *P. acuatum* n.sp., *P. pulvinum* n.sp., and *P. grac-*

TABLE 4. Summary of characters of species of *Pseudodistoma* recorded from Australia

Species	Biogeographic Range[1]	Range anticlockwise around Australia	Colony	Sand (embedded)	Stomach position (thirds of abdomen)	Length vascular stolon	Stigmata: maximum number/ row	Gonads: ♂ position in posterior abd.; ♀ relative to ♂	Embryos: maximum number; site of incubation[2]	Larva: trunk length (mm); adhesive organs	Other
P. gracilum n.sp.	A,te,tr	Kangaroo I. to Coral Sea	sessile cushion	none	middle	moderate	30	middle;anterior	1;bp stalks	1.75;short	mucus-like test
P. pulvinum n.sp.	A,te	"	"	"	"	"	30		"	?	—
P. aureum	WP,tr	Heron I. to Fiji	sessile cushion — mushroom	"	posterior	short	25	posterior;anterior	1–4;b	0.63;short stalks	—
P. inflatum n.sp.	A,te	NSW	"	centre of colony	"	"	20	anterior;amongst	?	?	sometimes surface lobed
P. pilatum n.sp.	A,te	Gt Australian Bight	stalks branched along length	"	middle	long	20	posterior;anterior	?	?	short, flat heads
P. acuatum n.sp.	A,te	"	"	layer beneath surface	"	"	8	posterior;?	?;bp	?	pointed heads
P. australe	A,te,tr	Exmouth Gulf to Port Phillip Bay	one or more lobes sessile or stalked joined basally	in stalk	"	"	25	posterior;anterior	1;bp	1.0;short stalks	few, short lateral larval ampullae
P. oriens n.sp.	A,te	Cockburn Sd to Port Phillip Bay	"	sometimes in stalk	"	"	30	"	1–2;b	1.35;sessile	"
P. candens n.sp.	A,te	Abrolhos to Pearson I.	stalked heads	"	"	"	25	anterior;amongst	1;b	1.5;long stalks	numerous long lateral larval ampulla

[1] A, indigenous; te, temperate; tr, tropical; WP, Western Pacific. [2] bp, brood pouch; b, no brood pouch.

ilum n.sp. and in *P. australe*, *P. cyrnusense*, *P. kanoka* and *P. fragile*, incubation of embryos is completed in a brood pouch constricted from the top of the abdomen, near the postero-dorsal corner of the thorax.

Brewin (1958 p.444) refers to 'bud like masses' that lie beneath the zooids of *Pseudodistoma cereum*; and in the present collection *Pseudodistoma oriens* n.sp. has juvenile replicate zooids in the stalk of a developing colony lobe. It therefore seems possible that replication does not involve the abdomen. However at this stage it is not clear whether it involves strobilation of the posterior abdomen (as in *Aplidium* spp.), or the posterior vascular stolon (as in Holozoidae).

Colonies of *Pseudodistoma* often (though not always) are stalked, with the zooids regularly arranged, the atrial apertures opening toward the top of the colony or the centre of the upper surface, and the branchial apertures toward the stalk or the outer margin. Colonies thus have colonial, but not cloacal, systems.

The zooids of most species of *Pseudodistoma* are basically similar to one another and this has resulted in confusion in their taxonomy. The zooids are, moreover, very muscular and preserved specimens usually are so contracted that details of their morphology, such as the numbers of thoracic muscle bands and stigmata, are obscured. When relaxed the posterior abdomen is long and narrow, but it is short and thick when contracted. There often is a vascular stolon of appreciable length with some longitudinal muscle fibres on it. Male follicles, when present, are either clustered in the posterior, middle or anterior third of the posterior abdomen, or spread out in longitudinal series. Sometimes the small ovaries are surrounded by the clustered male follicles but in other species they are anterior to them. The gut loop is very conservative — the quadrate stomach and rectal valve being present in most species (*P. fragile* being the exception). However there is some variation in the length of the oesophagus (see family discussion, above). At this stage, the larvae (which vary in numbers of ampullae), the position of the gonads, and the form and colour of the colony constitute the principal characters distinguishing species of this genus from one another.

Only one known species, *Pseudodistoma aureum* has a character that implies a polyphyletic origin for the genus, viz. tufts of columnar cells in the adhesive organs of the unusually small larvae rather than the everting, balloon-like organs of other species.

The majority of species are known from either Mediterranean, Japanese or southern hemisphere temperate waters. The type species is recorded from New Zealand. The only tropical species known are *P. brieni* Pérès, 1949 from Senegal and *P. aureum* (Brewin, 1957) from the Western Pacific (see below).

Although only one species from Australia (*P. australe* Kott, 1957) was previously regarded as indigenous, revision of the material has shown that all Australian species are (Table 4). As in *Sigillina*, it is probable that gene flow for many species is inhibited by the relatively large and few larvae, longer incubation and shorter free-swimming life, and the probability that the relative size of the trunk and tail are unlikely to enhance a long free-swimming life.

Key to species of *Pseudodistoma* recorded from Australia

1. Test soft, mucus-like ..... *P. gracilum* n.sp.
   Test firm, not mucus-like 2

2. Colonies flat-topped mushrooms or sessile cushions, the surface sometimes raised into lobes or swellings 3
   Colonies not flat-topped lobes or sessile cushions, usually with branched stalks 5

3. Sand embedded in test ..... *P. inflatum* n.sp.
   Sand not embedded in test 4

4. Embryos incubated in a brood pouch ..... *P. pulvinum* n.sp.
   Embryos not incubated in a brood pouch ..... *P. aureum*

5. Sand crowded in central or sub-surface test... 6
   Sand not crowded in central or sub-surface test 7

6. Sand in central test; head not pointed ..... *P. pilatum n.*sp.
   Sand in layer beneath surface; head pointed ..... *P. acuatum* n.sp.

7. Embryos in a brood pouch; stalk soft, fleshy ..... *P. australe*
   Embyros not in a brood pouch; stalk not soft, fleshy 8

8. Ovary anterior to testis follicles . *P. oriens* n.sp.
   Ovary surrounded by testis follicles ..... *P. candens* n.sp.

Species recorded from regions adjacent to Australia

Stalked species

Pseudodistoma africanum Millar, 1954 (see also Millar 1962) from Cape Province, South Africa, has a variety of colonies, probably not all conspecific, assigned to it. The Walker Bay (type) specimens have stalks tapering to the base, and resemble *P. oriens* n.sp. (see below) except for the sand embedded in the central test, and the spherical shape of the head of the South African species. The specimen from Natal (Millar 1962) with long tapering stalk has a smaller larval trunk than *P. oriens*.

Pseudodistoma antinboja Tokioka, 1949, from Japan (see also Nishikawa 1990, Rho 1971), has conical heads on short, thick, wrinkled cylindrical stalks and resembles the New Zealand *P. cereum*, differing in having only 8 to 9 stigmata per row (rather than 20 to 24). The Australian *P. australe* also is similar (see below).

Pseudodistoma arborescens Millar, 1967 from Madagascar, New Caledonia (Monniot 1987) and the Philippines (new records: QM GH456 GH471–3) has distinctive colonies of narrow, branching stalks with embedded sand, and soft, rounded or conical heads. Zooids have up to 15 stigmata per row, and a relatively long, narrow oesophagus, with the stomach in the posterior half to one-third of the abdomen. Larvae have a trunk 0.6mm long, deep pseudodistomid-like adhesive organs, and lateral ampullae.

Pseudodistoma cereum Michaelsen, 1924 (see also Brewin 1958) from New Zealand resembles *P. australe*, especially in its colour, it has similar wide, thick, short, stalks, 20–24 stigmata per row, and similar but smaller larvae with the trunk about 1.0mm long. It also differs in having a developmental sequence of up to 8 embryos in the top of the oviduct (Brewin, 1958) rather than the single one being incubated in the thoracic brood pouch in the Australia species (see below). It resembles, but is larger than, an undescribed tropical species from the Philippines (see *P. aureum* remarks, below).

Pseudodistoma novaezelandiae (Brewin, 1950), from New Zealand, has colonies with pointed lobes on short, thick stalks that resemble those of *P. cereum*, differing in the relatively long oesophagus with the stomach in the posterior third of the abdomen.

Pseudodistoma opacum (Brewin, 1950) from New Zealand has flat-topped, sessile lobes attached to basal test. These differ from the stalked lobes of *P. antinboja* Tokioka, which similarly has few stigmata per row. Like *P. novaezelandiae*, *P. opacum* has relatively long oesophagus.

Sessile species

Pseudodistoma brieni Pérès, 1949, from Senegal, forms massive, sessile lobes, rose-yellow or brown in life, with cartilaginous test. Zooids are numerous, irregularly placed. Twelve to 14 stigmata are in each row. A developmental sequence of up to 4 embryos are in the top part of the oviduct (as in *P. cereum*) which distinguishes the species from the Australian *P. pulvinum* n.sp. (see below) which has similar colonies. The larval trunk is probably about 1.0mm long and the larvae look like those of *P. australe*.

Pseudodistoma cyrnusense Pérès, 1952, from Corsica is yellow in life, with an orange pigment patch each side of the cerebral ganglion and one at the anterior end of the endostyle which distinguish the species from others (see *P. australe* n.sp., below).

Pseudodistoma fragile Tokioka, 1958, from Japan has soft mucus-like test that readily disintegrates as in *P. gracilum* n.sp. The Japanese species has up to 5 embryos being incubated in a brood pouch rather than only the one found in the Australian species.

Pseudodistoma kanoko Tokioka and Nishikawa, 1975, from Okinawa has massive sessile colonies, with translucent, firm test, red with white patches around zooid openings. Zooids have weak longitudinal muscles on the thorax, and 10 stigmata per row. Embryos are incubated in the posterior abdomen, sometimes projecting from it, and larvae have a trunk 2.1mm long with the tail and atrial siphon apparently displaced. Zooids of *P. australe* have lighter yellow patches anteriorly, but these are at the top of endostyle and between the apertures rather than surrounding them. A specimen with a leathery tapering stalk was assigned to *P. kanoko* (see Nishikawa and Tokioka 1976), but there is insufficient information to establish whether it is a normal variation in colony form or a different species related to *P. africanum* or *P. oriens* n.sp.

Pseudodistoma acuatum n.sp.
(Fig. 15. Plate 3b)

DISTRIBUTION

TYPE LOCALITY: South Australia (Ward I., 20-25m, coll. S. Shepherd 31.3.82, holotype SAM E2120 *QM GH923*; Ward I., on undercuts and ledges, 8m, coll. N. Holmes 12.4.83, photo 0064 R893, paratype QM GH2323).

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: The colonies, up to 10cm high, consist of a basal primary trunk, secondary, and tertiary branches (the terminal pointed lobes), each of about the same length (3cm). The colonies are firm throughout, and have a layer of sand embedded beneath the surface of the colony. The branches are crowded and vertical. Sand is absent from the central test. Zooids are crowded and project through the sand to open around the sides of the terminal lobes of the colony. Living colonies are white.

INTERNAL STRUCTURE: The zooids are very long, extending down through the stalk to the base of the colony. Fine longitudinal muscles extend the whole length of the zooid, and terminate each side of the tip of the posterior abdomen. The pharynx is narrow, with only about 8 stigmata per row. The oesophagus is relatively long, the stomach being in the middle of the posterior half rather than in the middle third of the abdomen. It is smooth walled, and quadrate in section. the male follicles are in the posterior end of the posterior abdomen.

A single embryo is incubated in a brood pouch projecting from the zooid at the top of the abdomen in specimens collected in January.

REMARKS

These stalked colonies have a superficial resemblance to *P. cereum*, however they have longer and more pointed heads and branching, rather than simple cylindrical stalks. The sympatric species *Pseudodistoma pilatum* n.sp. has sand throughout the centre of the colony (rather than confined to a layer beneath the surface as it is in the present species), its stalks are thicker, shorter and not as long as those of the present species, the terminal expanded head has a more or less flat upper surface (where the zooids open) rather than being long and pointed, and it has more numerous stigmata.

Pseudodistoma aureum (Brewin, 1957)
(Fig. 16)

Sigillinaria aurea Brewin, 1957, p.580.
Pseudodistoma aurea: Kott, 1981, p.157. Nishikawa, 1984a, p.114. Monniot and Monniot, 1987, p.81.

FIG. 15: *Pseudodistoma acuatum* n.sp. — **a**, part of colony (holotype SAM E2120); **b**, zooid (paratype QM GH2323). Scales: **a**, 1cm; **b**, 0.5mm.

DISTRIBUTION

NEW RECORDS: Queensland (Capricorn Group, QM GH4958 –73 GH5103 GH5177 GH5199 GH5206 GH5259 GH5502 GH5691).

PREVIOUSLY RECORDED: New Zealand (North I. — Brewin 1957). Fiji (Dravuni — QM GH106 Kott 1981). Majuro Atoll (Nishikawa 1984a). French Polynesia (Monniot and Monniot 1987).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are sessile, flat-topped pillow-, or mushroom-shaped, to 2cm high and 3cm diameter, sometimes narrowing to a short stalk from the lower surface. The test is firm, transparent in preservative with zooids evenly distributed in it. Each zooid opens (on the upper surface only) by 2 apertures. In living colonies the test is transparent, 'orange buff', 'ochraceous buff', 'tawny ochraceous', 'buff yellow', 'maize yellow', 'Indian yellow', 'deep chrome', 'chrome yellow', 'orpiment orange', 'cadmium orange', 'vinaceous pink', or 'saturn red' (Ridgeway 1886). Occasionally there is a honeycomb pattern, of 'orange ochraceous' (blood?) around the zooids. Zooids are opaque, and usually a darker shade of the same colour as the test. One collector (PK) has referred to the appearance of these colonies as 'orange ice' or 'soft orange look'.

INTERNAL STRUCTURE: Zooids are long (about 8mm) and slender. Anteriorly they project slightly from the upper surface and posteriorly they extend into the base of the colony and into the stalk (when one is present). The thorax and abdomen together are only about 2mm long, the remainder of the length consisting of posterior abdomen. Only very short vascular stolons are present at the posterior end of the zooid. The atrial siphon is sometimes longer than the branchial one. About 12 longitudinal muscles extend along each side of the thorax and along the abdomen and posterior abdomen which, when muscles are contracted, may be drawn up behind the abdomen in a short, blunt appendage no longer than the abdomen. About 25 stigmata are in the anterior rows, the dorsal end of each row extending anteriorly along each side of the dorsal mid-line. The posterior and middle rows each have 20 stigmata.

The oesophagus is relatively long, and the short, smooth-walled stomach with the usual 4 compartments is two-thirds to three-quarters of the distance down the abdomen. The duodenal area is relatively short. An oval posterior stomach is in the pole of the gut loop. The testis follicles are in a single series in the middle of the posterior third of the posterior abdomen, and the small ovary is just anterior to the male follicles. Up to 4 embryos are present in a developmental series in the distal part of the oviduct (in the thorax and at the top of the abdomen) in specimens collected in May, October and November, but not in January, April, August, or September. Gonads were not present in the small colonies taken in April

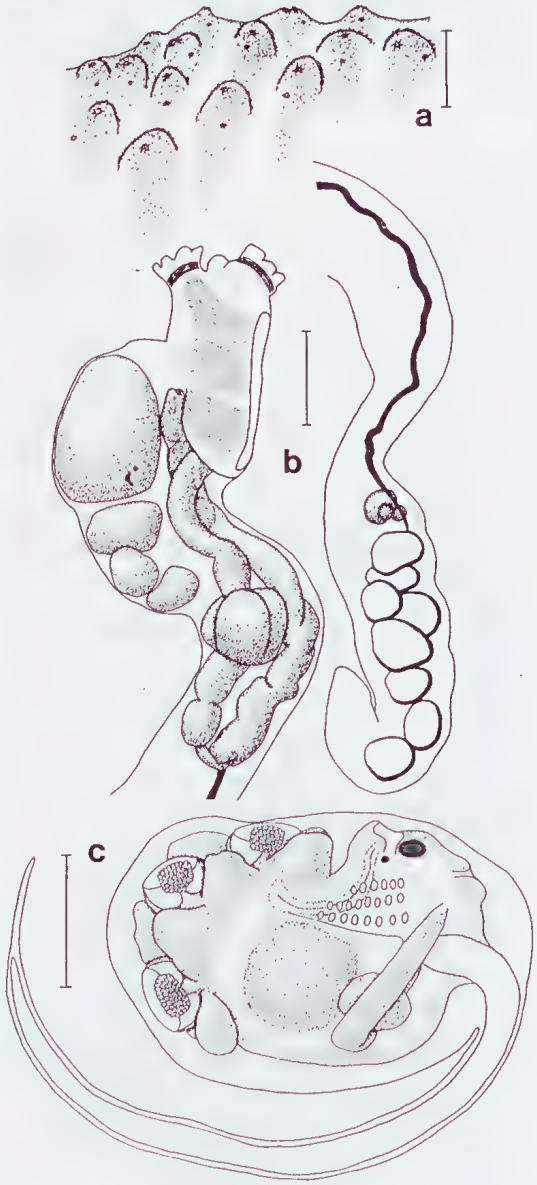


FIG. 16: *Pseudodistoma aureum* — **a**, part of colony surface (QM GH4958); **b**, zooid (QM GH4970); **c**, larva (QM GH4970). Scales: **a**, 2mm; **b**, 0.5mm; **c**, 0.2mm.

and August. A colony taken in September has male follicles but no ovary, and it is possible that the species is protandrous.

Larvae are relatively large, the trunk being 0.6 to 0.65mm long. The tail is wound slightly more than halfway around it. The 3 median adhesive organs are on short thick stalks, and four rounded lateral ampullae are on each side of the anterior mid-line. The axial cone of adhesive cells has a narrow stalk attaching it to the base of the epidermal cup, and it has a tuft of what appear to be columnar cells diverging out from the base to a flat terminal platform.

REMARKS

Characteristic of the present species is the relatively clear, transparent test and the rounded cushion-like colonies. The oesophagus described for the New Zealand colonies (Brewin 1957) is longer than that in the present material, and the duodenal region between the stomach and mid-intestine appears to have been overlooked. In all other respects, however, zooids, colony and larvae from the type material are the same as those from Fiji (Kott 1981), French Polynesia (Monniot and Monniot 1987) and Heron I.

The firm, clear, golden colonies are readily distinguished from other species of *Pseudodistoma*. The zooids also differ from most other species in their relatively long oesophagus, short vascular stolons and small larvae with a tuft of columnar cells rather than the thin-walled everting balloon of other species. *Pseudodistoma cereum* has a similar larva of about the same size, but a short oesophagus (see Brewin 1958) and stalked colonies; *P. novaezelandiae* has a longer oesophagus, but also has stalked colonies; and *P. opacum* (Brewin, 1950) has a longer oesophagus, but lobed colonies and only 9 or 10 stigmata.

Of the known indigenous Australian species the oesophagus is a similar length in *P. inflatum* n.sp., which can be distinguished by its less regular, opaque orange colonies with sand in the base, and gonads in the anterior half of the posterior abdomen. *Pseudodistoma arborescens* Millar, 1967 from Malagasy, New Caledonia and the Philippines (new records: QM GH456 GH471–3) has a similar long oesophagus, and gonads in the posterior end of the posterior abdomen but is distinguished by its colony, with rounded to conical heads on long branched stalks.

Pseudodistoma australe Kott, 1957
(Fig. 17. Plate 3c,d)

Pseudodistoma australis Kott, 1957, p.101; 1963, p.78; 1972b, p.172 (part, not specimens from Waldegrave I. < *Sigillina grandissima* Kott).
Pseudodistoma cereum: Kott 1972a, p.12.

DISTRIBUTION

NEW RECORDS: Western Australia (Exmouth Gulf, QM G9289 G9290 G9473; Shark Bay, WAM 867.83 *QM GH2133*, WAM 1018–9.83; Houtman's Abrolhos, WAM 764.82 814.83 950.83 1015.83 198.87 198.88 234.88 238.88; Cockburn Sound, WAM 152.75 928.89). South Australia (Great Australian Bight, QM GH4160; Cape Jaffa, SAM E2486). Victoria (Port Phillip Head, QM GH51).

PREVIOUSLY RECORDED: Western Australia (Rottnest I.— holotype AM Y0919, AM U3982–3 Y1314 Kott 1957 1963). South Australia (Elliston Bay — SAM E2549 Kott 1972b; Nora Creina Bay — SAM E2440 Kott 1972a).

DESCRIPTION

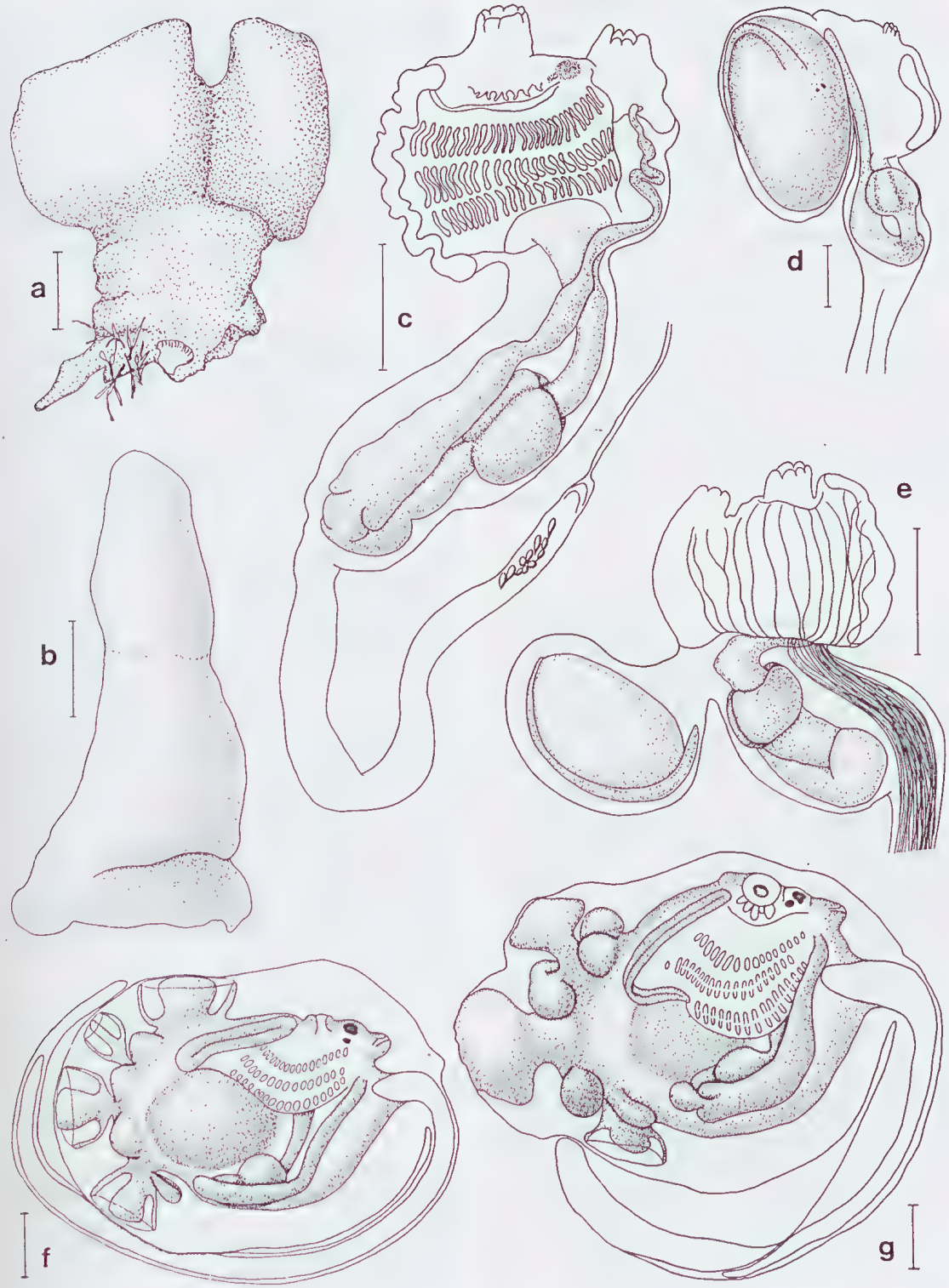
EXTERNAL APPEARANCE: The colonies are stalked or sessile, conical to rounded fleshy lobes or stalked heads arising from a common basal test mass or upright fleshy stalk. The zooids open all around the lobes but not on the common base or stalk.

The smaller conical heads (about 1.5cm long) on relatively long (to 2.5cm) narrow stalks (WAM 1015.83) probably are younger colonies than those in which the almost sessile heads, up to 5cm, are on a fleshy basal test mass to 1.5cm high (WAM 867.83). The test is very soft but fibrous, and firmer in the stalk than the head. The stalk contains scattered sand grains. In preservative the colonies are often very squashed.

In life, the head is rose-pink to red-orange, with the outer layer of test translucent and a white to yellow opaque ring around the rim of each aperture. The stalk is brown. Zooids are orange in preservative, fading to whitish-beige. The white particles that form the opaque ring around the apertures persist in the surface test around the apertures.

The laterally flattened specimens from South Australia (SAM E2486) have a patch of yellow or brown pigment over the dorsal tubercle. The faded, preserved zooids of the holotype colony have an opaque, white, circular patch in the same

FIG. 17: *Pseudodistoma australe* — **a**, **b**, colonies (**a**, QM G9473; **b**, WAM 859.83); **c–e**, zooid and parts of zooids (**c**, **e**, holotype AM Y919; **d**, WAM 152.75); **f**, **g**, larvae (holotype AM Y919). Scales: **a**, **b**, 1cm; **c–e**, 0.5mm; **f**, **g**, 0.2mm.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position over the dorsal tubercle. Similarly, there are yellow spots over the dorsal tubercles of the orange lobed colony photographed at Exmouth Gulf (AMPI 76, Plate 3c).

INTERNAL STRUCTURE: Contracted, the thorax and abdomen together are sometimes only about 1.5mm long. The posterior abdomen is straplike, and about the same length. However, in less contracted zooids the posterior abdomen and delicate vascular stolon extend down into the stalk of the colony and zooids are long and threadlike, most of their length being posterior abdomen. Longitudinal muscle bands (from 12 to 20 on each side) extend along the length of the zooid, half from the atrial and branchial siphons and about half from the anterior part of the ventral border (across the endostyle). They terminate at the end of the posterior abdomen. The branchial tentacles are in about 4 rows, the 6 largest ones in the posterior circle. The branchial sac is wide, with 22 stigmata in the second and third rows, and about 25 in the anterior row, which is deflected anteriorly along the dorsal midline.

The oesophagus is moderately long. The stomach, divided into 4 longitudinal quarters by shallow grooves in its otherwise smooth wall, is about halfway down the abdomen. The duodenal area is long, an oval posterior stomach interrupts the narrow mid-intestine in the pole of the gut loop. A rectal valve at the proximal end of the ascending limb of the gut loop separates the mid-intestine from the rectum. The anus, with a bilabiate border, opens halfway up the branchial sac.

A short double series of small male follicles were observed in the posterior end of the posterior abdomen in the holotype, although they are half to three quarters of the way down the posterior abdomen in the South Australian specimens (SAM E2486).

A single series of about 8 mature male follicles are present about two-thirds of the way down the contracted posterior abdomen in a mature colony from Exmouth Gulf collected in August (QM G9473). They are flattened against one another into discs, but this may not be their shape when the zooid is extended. Zooids in a colony off Rottnest have a single embryo being incubated in the oviduct at the top of the abdomen, just behind the postero-dorsal corner of the thorax. The large embryo protrudes from the zooid, distorts the thorax, and is partially constricted off from it.

The larval trunk is 1.0mm long and the tail wound halfway around it. It has 3 large, stalked adhesive organs in the anterior mid-line, each consisting of an ectodermal cup around a large hollow eversible axial cone or platform, all on a long narrow stalk. Four wide ampullae alternate with the adhesive organs. These are flattened antero-posteriorly and are produced laterally on each side into rounded lobes that curve ventrally, forming a cushion around the stalks of the adhesive organs. There is an ocellus and an otolith. In some zooids of colonies collected in November and December (AM Y919, U3982) a single embryo is present in a brood pouch, partially constricted off from the top of the abdomen. Ova were not detected in any of the other colonies.

REMARKS

The type colony, although mutilated, appears to have been stalked rather than the investing cushion which Kott (1957) thought it to be.

The species resembles *P. cereum* from New Zealand, which has similar stalked colonies although the heads are regular and rounded; and although its larvae are also similar they are smaller (trunk 1mm long). Some of the colonies resemble some of those of *P. africanum* Millar, 1954 which are also said to be pink in life (see Millar 1962). However the head and stalk of South African material remain distinct, in even the largest colonies, and the long sessile lobes found in the present species do not develop. Two sessile colonies from Western Australia differ from the present species in having sand in the stalk, and larger larvae without ampullae around the sessile adhesive organs; and in lacking a distinct brood pouch constricted off from the abdomen. They have been assigned to *Pseudodistoma oriens* n.sp. (WAM 859.83 923.83).

Pseudodistoma cyrnusense from Corsica is a sessile species with pigment patches in a similar position to the present species. However the Corsican species has 2 (one each side of the dorsal tubercle) rather than the single median one of *P. australe*.

Pseudodistoma candens n.sp.
(Fig. 18. Plate 3e,f)

Pseudodistoma cereum: Kott, 1975, p.4.

DISTRIBUTION

TYPE LOCALITY: South Australia (Pearson I., coll. S.A. Shepherd 28.3.82, holotype QM GH977, paratype SAM E2118).

FURTHER RECORDS: Western Australia (Cervantes, WAM 197.87; Dongara; Cockburn Sound, WAM 70.75 .841.83 *QM GH2132*, WAM 1014.83 QM GH5462). South Australia (Cape Jaffa, SAM E2117

E2119 E2446 E2526, QM G9286 Kott 1975); Ward I., QM GH1295; Topgallant I., QM GH972; Hotspot, QM GH2421; Nuyts Archipelago, SAM E2408); Victoria (Cape Nelson, SAM E2407).

Description

External Appearance: Colonies are long (to 5cm) and oval (to 2cm diameter), to short and rounded (to 3cm diameter) or conical and sometimes laterally flattened heads, usually on a thick (1cm diameter) stalk of variable length (to 5cm), sometimes tapering to the base. It is always tough, leathery and transversely wrinkled. The head sometimes overlaps the top of the stalk. On the head the test is tough, in larger specimens almost opaque, and more or less smooth on the surface with cloudy brown pigment cells.

The stalked heads often appear to be solitary, but occasionally the stalk is branched. Replicated zooids with small abdomina sometimes are present in the stalk and appear to move up into the head as it develops. The zooids open all around the outer surface of the head. Living specimens are said to be wine red, although the colour appears to be in the zooid, and the test is translucent. In photographs of a living specimen (Pl. 3e,f) fine red bands are present around each aperture. In preservative the zooids are yellow but subsequently fade to white.

Internal Structure: The zooids are up to 2cm or more, although most of their length is taken up by the posterior abdomen, and the thorax and abdomen are together only about one to 2mm. There is a long (up to 2cm) vascular stolon extending posteriorly from the end of the posterior abdomen. Twenty to 40 longitudinal muscles extend the length of the zooid and some of these extend along the length of the vascular stolon. The branchial and atrial lobes are especially conspicuous. Up to 20 long, rectangular stigmata are in each of the second and third rows, and in the anterior row additional stigmata extend forward along each side of the mid-dorsal line. The stomach has the usual 4 longitudinal compartments. A long, duodenal area and oval posterior stomach are in the distal part of the descending limb of the gut loop. The heart is a U-shaped tube at the end of the posterior abdomen.

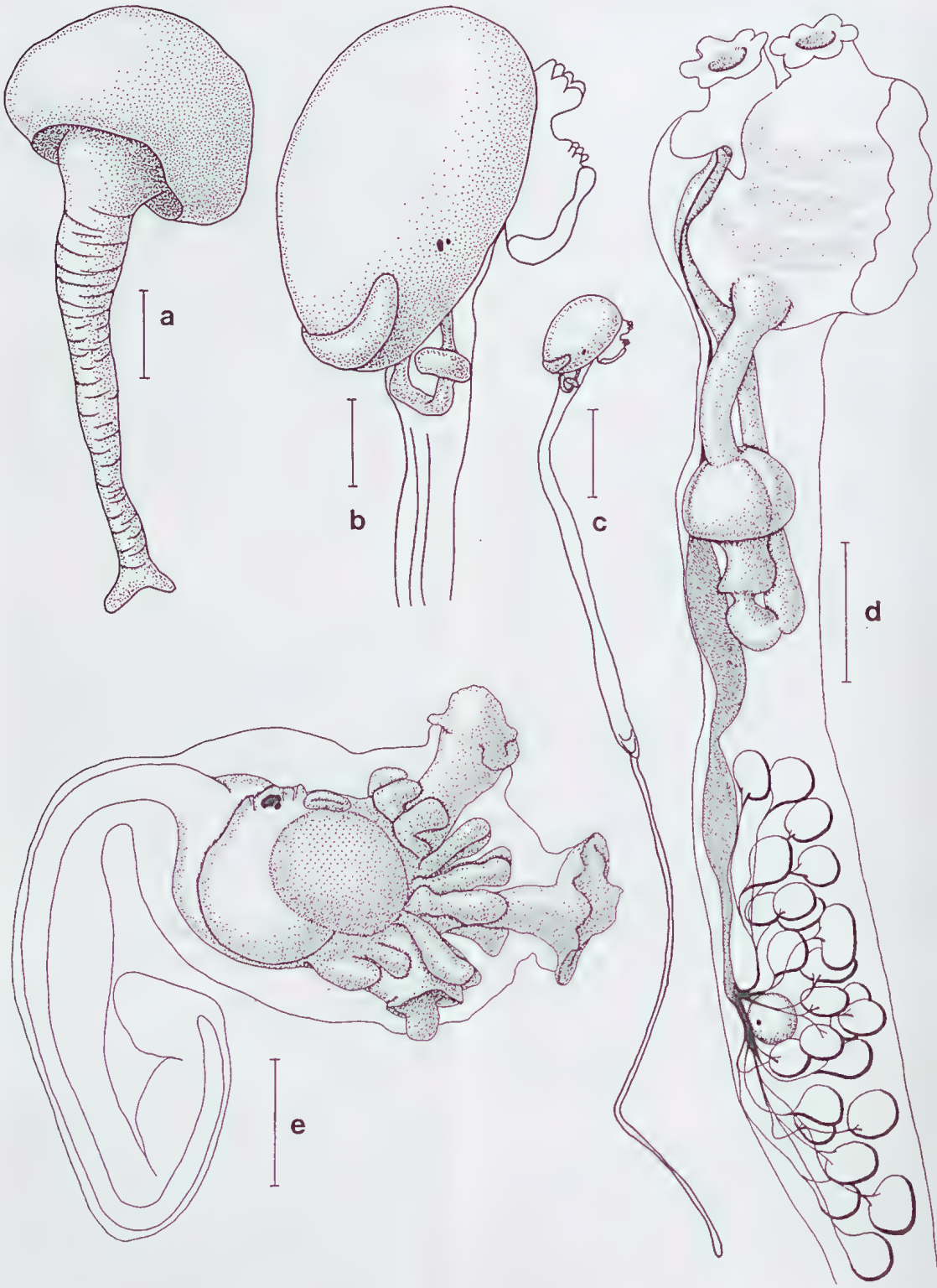
The gonads are in the anterior part of the posterior abdomen just behind the gut loop. The testis follicles are large and pear-shaped and are in a long, loose or a tightly bunched cluster around the small ovary. The vas deferens is long, extending from halfway down the side of the male follicles to a point level with the ovary, where it is joined by the vasa efferentia from the follicles. The length of the testis probably depends on the state of contraction of the posterior abdomen. A single large embryo is found in the oviduct at the top of abdomen in the holotype. Some specimens (QM GH972) collected in March from South Australia have a conspicuous egg in the posterior abdomen but male follicles are not developed. Mature male follicles are in specimens from Point Peron (WAM 70.75) collected in April and from Cervantes I. (WAM 189.75) collected in May. Large larvae (1.5mm trunk) project from the side of the zooid along the length of the oesophagus to just behind the atrial cavity in specimens collected from Pearson I. in March (QM GH977). Larvae have 3 large, stalked eversible adhesive organs in the midline anteriorly. The axial protrusions are rounded and the everted organs seem to expand into thin-walled balloon-shapes. About 8 long, digitiform ectodermal ampullae per side bend anteriorly at right angles to lie parallel to the stalks of the adhesive organs. The tail winds three-quarters of the way around the trunk. An ocellus and otolith are present.

Remarks

Pseudodistoma africanum Millar, 1954 (also Millar 1962) from South Africa, has rounded heads on stalks tapering toward the base, as in the present species. With the exception of one specimen from Natal which is 8cm long and may be a different species (Millar 1962), the African species has smaller colonies, softer stalks without an outer leathery cuticle, and less muscular zooids with only about 8 longitudinal bands. The large specimen from Natal more closely resembles *P. candens*, having about 20 longitudinal muscles. However its larva is smaller (1mm long trunk).

Pseudodistoma cereum Michaelsen, 1924 from New Zealand, has shorter, fleshy and cylindrical stalks (see Brewin 1958) rather than the long ones of *P. candens*.

The present species does not have sand included in its test, and thus is distinguished from other Australian stalked species (e.g. *Pseudodistoma pilatum* n.sp., *P. acuatum*). The species most readily confused with the present one is the sympatric *Pseudodistoma oriens* n.sp., which sometimes has long tapering, leathery, wrinkled stalks like the present species. *Pseudodistoma oriens* has pointed conical heads rather than rounded ones, softer more transparent test on the head, and slightly larger zooids. It also has larger larvae with sessile (rather than stalked) adhesive organs, a long irregular series of testis follicles in


a
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e

the posterior half of the posterior abdomen and separated from the ovary (rather than being bunched around the ovary in the anterior half as they are in *P. candens*), and a wide band of strong muscles on the vascular stolon. Colonies of *P. candens* from off Cape Jaffa may be found to be a separate species. However they differ from the type only in their darkly pigmented zooids, thick fleshy stalks, and large opaque flattened heads, and for the present they have been assigned to *P. candens*.

Pseudodistoma gracilum n.sp.
(Fig. 19. Plate 4a–e)

Pseudodistoma cyrnusense: Kott, 1972b, p.173.
Pseudodistoma cereum: Kott, 1976, p.58.
Pseudodistoma fragile: Monniot, 1987, p.508.

DISTRIBUTION

TYPE LOCALITY: South Australia (Top Gallant I. 10m, coll. S. Shepherd March 1982, holotype SAM E2413 *QM GH971*; Grindal I., coll. W.H. Sasse 6.4.87, paratype QM GH4167).

FURTHER RECORDS: South Australia (Top Gallant I., QM GH973; Investigator Group, QM GH2422; Elliston Bay — SAM E2414 Kott 1972b; Beachport, SAM E2412; Kangaroo I., QM G11989; Cathedral Rock, QM GH4158). Victoria (Western Port —MV F57789 Kott 1976). New South Wales (Jervis Bay, QM G10092; Port Jackson AMY2263). Queensland (Heron I. QM GH4954; Lizard I., QM GH3808; Lihou Reef, QM GH4955; northern Great Barrier Reef, QM GH5334).

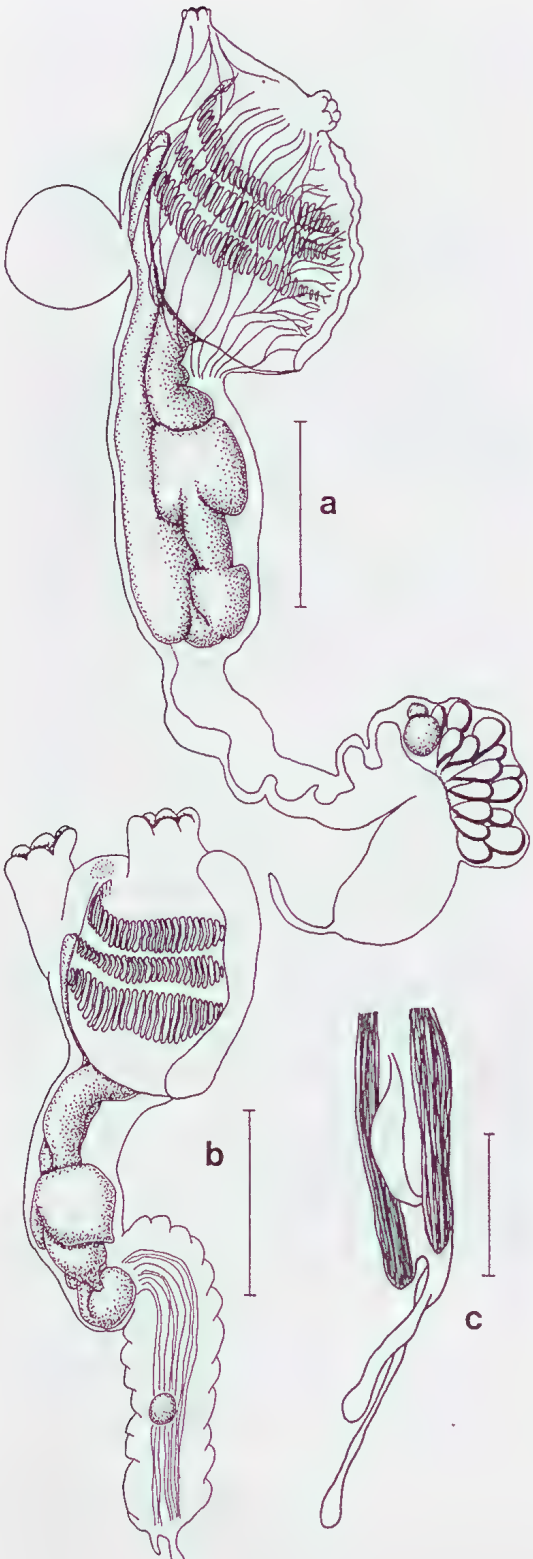
DESCRIPTION

EXTERNAL APPEARANCE: The test is mucus-like and disintegrating in preservative, often with the zooids lying free and the colonies so soft and flaccid their shape cannot be seen. In preservative all colonies are pale cream with beige zooids and contain evenly distributed cloudy morula cells in the test.

In photographs of some living specimens (QM GH4167 GH5334) the test is colourless and the extended zooids show as white streaks converging into the centre of the colony. The collectors notes record the holotype specimen to have had a 'colourless matrix with cream zooids'. However a colony (QM GH973) taken from the holotype location at the same time (March 1982) but at a greater depth (20m rather than 10m) is said to have been 'dark green with blue zooids'. One colony is recorded by the collector to have been a 'white jelly-like ascidian', but the photograph of the specimen (QM G11989) *in situ* has pale violet zooids, and a photograph from the same location shows white streak-like zooids in a colourless test (AMPI 223). The specimen from Cathedral Rock (QM GH4158) appears from its photograph to be bluish-purple like the Kangaroo I. specimen (QM G11989). Other collectors report living colonies with 'black-purple zooids' (QM G10092), and white zooids in 'a very fluid pale brown gel' test (QM GH3803). One living colony is reported to have been a 'fragile gelatinous mass about 50cm square and 3cm thick under a large rock' (QM G10092). The colony from Lihou Reef is saucer-shaped (QM GH4955). Only one bluish colony from South Australia (QM GH4158), in which zooids are in a vegetative condition, has relatively firm test and the colony entire in preservative. From photographs, colonies vary from spherical to extensive masses with the surface produced into lobes.

INTERNAL STRUCTURE: Zooids are robust up to 3cm long, most of the length being a narrow thread-like posterior abdomen. Thorax and abdomen are together about 3mm long, the thorax slightly longer than the abdomen when relaxed. The atrial siphon is sometimes longer than the branchial siphon, but sometimes the whole dorsal surface of the zooid swells out behind the atrial aperture forming a conical projection. Each aperture has 6 well-defined, evenly rounded lobes around its rim. From 12 to about 20 longitudinal muscles are on the thorax, and extend along each side of the abdomen and posterior abdomen. Fine transverse branches from the ventral longitudinal muscles terminate along each side of the endostyle. The longitudinal muscles terminate posteriorly in well-defined horns each side of the heart at the end of the posterior abdomen. Muscles do not extend onto the one to 4 fine vascular stolons, which vary from short to moderately long. Stigmata are from 0.4mm to twice that length, depending on the state of contraction of the thorax. They reduce in length at the ventral end of each row. From 20 to 25 stigmata are in the second and third rows and about 25 to 30 in the anterior row (which deflects anteriorly along the mid-dorsal line).

FIG. 18: *Pseudodistoma candens* n.sp. — **a**, colony (holotype QM GH977); **b–d**, zooids and parts of zooids showing embryos being incubated, proportions of zooids, relatively long vascular stolon, bunched testis follicles surrounding ovary, and distended vas deferens (**b–c**, holotype QM GH977; **d**, QM GH5462); **e**, larva (holotype QM GH977). Scales: **a**, 1cm; **b**, **d**, 0.5mm; **c**, 2mm; **e**, 0.4mm.



The smooth-walled stomach halfway down the abdomen is partially divided into 4 broad, shallow longitudinal compartments. An oval posterior stomach is in the pole of the gut loop. A distinct rectal valve is at the proximal end of the ascending limb of the gut loop. A bunch of pyriform male follicles is about three-quarters of the way down the posterior abdomen or sometimes in the posterior quarter. A small ovary is anterior to the male follicles in a specimen collected in April (SAM E2412 from South Australia) and from Lihou Reef (QM GH4955: unknown date). These colonies have a single round embryo in the brood pouch constricted off from the top of the abdomen. Embryos were not in other examined material.

The single larva in each brood pouch of specimens from New Caledonia (Monniot 1987) has the tail wound halfway around the 1.75mm long trunk, and, like larvae of *P. aureum*, has deep conical adhesive organs, 2 lateral ampullae and median dorsal and ventral ampullae.

REMARKS

A specimen of this species (QM G10092) analysed for vanadium was found to have 800–1600 ppm (Paul Fredrickson *pers. comm.*).

The species has a range in the number of stigmata but neither this nor any other morphological or geographical feature has been identified to correlate with colony appearance in photographs. However, it is not known what the colonies with zooids fully extended and appearing as white streaks would look like when contracted. Further, the zooids of colonies appearing as blue-purple in photographs always are contracted (in one case they also are in their vegetative phase). Possibly when extended they would appear as characteristic white streaks in colourless test.

Pseudodistoma fragile: Monniot 1987 seems not to be distinct from the present species. Monniot has recorded about 40 stigmata, although in the figured specimen (Monniot 1987, Fig. 5A) they are not so numerous, being near the top of the range recorded for the Australian specimens (see QM GH4167 from South Australia and QM

FIG. 19: *Pseudodistoma gracilum* n.sp. — **a**, zooid showing fine transverse branches from ventral longitudinal muscles, bunched male follicles and ovary halfway down posterior abdomen, and brood pouch (QM GH4955); **b**, contracted zooid (QM G10092); **c**, posterior end of posterior abdomen showing heart, the insertion of the longitudinal muscles, and vascular appendices (QM G11989). Scales: **a**, **b**, 1.0mm; **c**, 0.5mm.

FIG. 20: *Pseudodistoma inflatum* n.sp. — zooid (QM G9636). Scale: 1mm.

GH4955 from Lihou Reef in the Coral Sea). The fact that one of the colonies with the maximum number of stigmata is from southern Australia and the other from the Coral Sea tends to support the view that the New Caledonian and Australian specimens are conspecific.

Pseudodistoma fragile Tokioka, 1958 (from Japan) has similar fragile colonies and similar zooids to the present species. However, the Japanese species has greenish-yellow (rather than blue or white) living zooids, the long curved brood pouch contains up to 5 embryos (rather than one), and the larvae have a trunk 2.3 to 2.6mm long (instead of 1.75mm in the New Caledonian specimen). Apart from the size difference, the larvae of the Japanese species and the present one are similar. Larvae with a large trunk are not unusual in this genus, but the absence of median ampullae and the limited number of lateral ampullae is.

Pseudodistoma inflatum n.sp.
(Fig. 20. Plate 4f)

DISTRIBUTION

TYPE LOCALITY: New South Wales (South Solitary Is. rock faces 10m, coll. N. Coleman 27.9.76, AMPI 184, holotype QM G10157; Julian Rocks, Byron Bay, reef, 15m, coll. N. Coleman 29.3.75, AMPI 158, paratype QM G9472).

FURTHER RECORDS: New South Wales (Byron Bay, AM Y2002; Coffs Harbour, QM G9636). Queensland (Ngeering Reefs off Mooloolabah, QM GH5666–7).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies, to 3cm in maximum extent and 2cm high, are flat-topped and mushroom-like or sessile cushions with rounded margins, or wedge shaped narrowing to the upper free margin. The surface sometimes is raised into ridges and rounded to conical elevations, or divided into flat-topped lobes. Sand is present in the centre of the colony, just beneath the surface in the base, becoming less crowded and removed from the surface toward the top of the colony. Sand always is absent from the surface layer of test, which is opaque (in preservative) and contains a white cloudy suspension.

Living colonies are opaque, orange-red over each zooid and bright yellow between them. In preservative they are grey and firm.

INTERNAL STRUCTURE: Zooids are small and slender, often less than 1cm long when contracted. Atrial and branchial siphons are about the same size, and both apertures are bordered by 6

well defined rounded lobes. The longitudinal muscles extend in a wide band along each side of the abdomen and posterior abdomen. The heart is at the posterior and of the posterior abdomen the vascular stolon is relatively short.

There appear to be about 20 stigmata per row, however the exact number could not be determined owing to contraction of the thorax. The oesophagus is long, and the conspicuously 4-chambered stomach is in the anterior half of the posterior third of the abdomen. Gonads, when present, are in the anterior half of the posterior abdomen, the testis follicles in 2 clumps, one anterior and one posterior to a large ovum. Sometimes the anterior clump of testis follicles extends up into the abdomen alongside the gut loop. However in other specimens there is a gap between the anterior testis follicles and the posterior end of the abdomen. Larvae are not known.

REMARKS

This species appears to be indigenous to the southern (temperate) half of eastern Australia. Like the tropical species *P. aureum* and *P. arborescens* Millar, 1967, and *P. opacum* and *P. novaezelandiae* (from New Zealand), it has a long oesophagus. It most closely resembles *P. aureum* from which it is distinguished by its irregular opaque colonies with sand in the basal half, and the posterior position of its gonads.

Pseudodistoma oriens n.sp.
(Fig. 21. Plate 5a)

Pseudodistoma cereum: Kott, 1972b, p.173 (part, not specimens from Elliston Bay < *P. pilatum* n.sp.).

DISTRIBUTION

TYPE LOCALITY: Victoria (Port Phillip Heads Channel, 20m very fast current, on ledges, common, coll. J.E. Watson 25.11.76, holotype MV H306; paratypes QM GH4953).

FURTHER RECORDS: Western Australia (Rottnest I., WAM 859.83 *QM GH2134*; Geographe Bay, WAM 923.83). South Australia (Waldegrave I. — SAM E2115 E2116 Kott 1972b; off Cape Jaffa, SAM E2525; St. Vincent Gulf, QM G9287). Victoria (Port Phillip Heads, QM GH116).

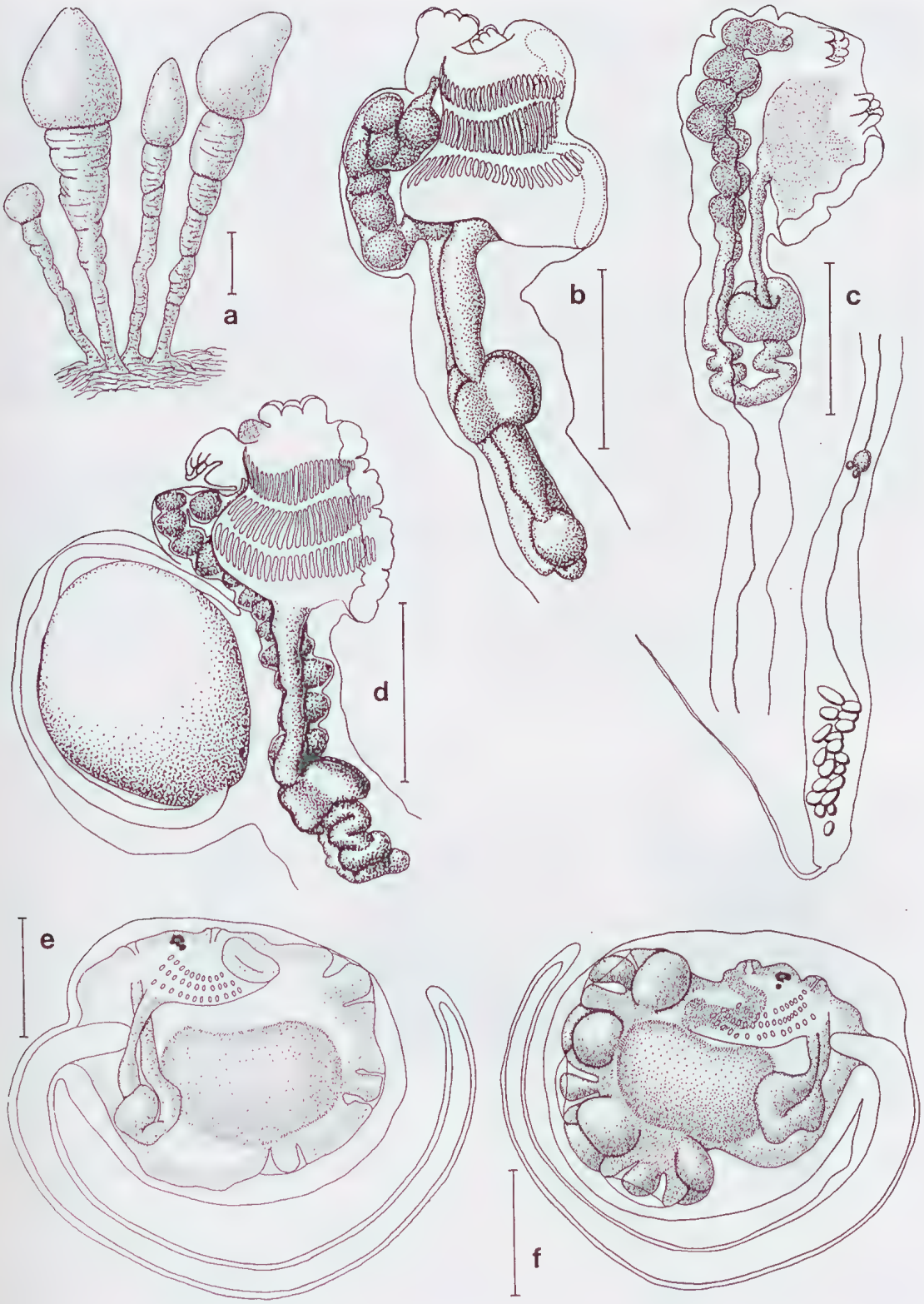
DESCRIPTION

EXTERNAL APPEARANCE: Colonies consist of stalked, pointed heads (up to 6cm long), the stalk usually longer than the head. Although most of the specimens in the examined material are solitary, the holotype has a number of stalked heads attached to a basal membrane. Stalks are up to 10cm long. Usually they are leathery and wrinkled with an outer hard cuticle, tapering to the base (MV H306, QM GH4953, SAM E2115 E2116). A few of the specimens have short, cylindrical stalks with some embedded sand (WAM 859.83 923.83). Zooids are conspicuous with the atrial openings toward the free end of the head. The branchial openings are closer to the stalk. The zooids bend at right angles so that, despite the orientation of the thoraces, the posterior ends extend down into the stalk, as is usual for most stalked aplousobranch species (Kott 1989).

Living colonies are said to be 'horizon red'. In preservative the test is translucent and the zooids pink to orange, subsequently fading to opaque cream.

INTERNAL STRUCTURE: Zooids are small, the thorax and abdomen (contracted) together are about 1mm long but about 3 times that length when partially relaxed (SAM E2115). About 20 longitudinal muscles extend along each side of thorax, abdomen and posterior abdomen. On the posterior abdomen the longitudinal muscles are in a wide, conspicuous band along each side and these continue onto the vascular stolon. Unperforated pharyngeal areas are anterior and posterior to the 3 rows of stigmata. The 2 posterior rows each have about 22 stigmata and the anterior row has an additional 5 or 6 perforations continuing anteriorly along the mid-dorsal line. The stomach, with the usual 4 longitudinal grooves, is halfway down the abdomen, and a long duodenal region and an oval posterior stomach are in its posterior half. A narrow mid-intestine is in the pole of the gut loop. A rectal valve is at the base of the ascending limb of the gut loop, which extends to about halfway up the thorax, ending in a bilabiate anus. Mature male follicles are in a long series in the posterior half of the posterior abdomen in specimens from Waldegrave I. collected in October (SAM E2116). The small (2 or 3 egg) ovary is anterior to the testis follicles and well separated from them. Immature follicles can

FIG. 21: *Pseudodistoma oriens* n.sp. — **a**, colony (holotype MV H306); **b**, zooid showing thorax and abdomen (paratype QM GH4953); **c**, zooid showing ovary about halfway down the posterior abdomen, and the narrow vascular stolon from the tip of the posterior abdomen (SAM E2116); **d**, zooid showing larva in brood pouch (paratype QM GH4953); **e**, **f**, larvae (WAM 923.83: **e**, less mature; **f**, mature). Scales: **a**, 2cm; **b**, **c**, **d**, 1mm; **e**, **f**, 0.4mm.


a
b
c
d
e
f

be seen irregularly branching off the vas deferens in the posterior half of the posterior abdomen in specimens from Hotspot collected in June (SAM E2115).

In the type material from Port Phillip Heads collected in November (MV H306; QM GH4953), and the specimen from Geographe Bay collected in January (WAM 923.83) there are one or 2 embryos being incubated in the distal part of the oviduct at top of the abdomen behind the postero-dorsal corner of the thorax. These embryos become very large, project from the side of the abdomen, and distort the zooid (the abdomen as well as the thorax). However there is no brood pouch constricted from the side of the zooid.

The larval trunk is variable, from 1.1 to 1.7mm long, and the tail winds three quarters of the way around it. A large, almost spherical yolk mass occupies a large part of the trunk, and the larval pharynx and gut are at the posterior end. An otolith and ocellus are present. The 3 median adhesive organs are large, sessile, consisting of an eversible, hollow axial cone depressed into the larval trunk. One mature larva from the specimen from Geographe Bay (WAM 923.83) has 5 adhesive organs, and 4 rounded ampullae from each lateral line. Other larvae examined from the same specimen lot lack the lateral ampulllae, and have the usual 3 adhesive organs.

Juvenile, presumably replicate, zooids are present in the stalk of a developing colony lobe.

REMARKS

Pseudodistoma oriens has long-stalked colonies like those of many specimens of *P. candens*, zooids have a similar long vascular stolon behind the posterior abdomen, and the species are sympatric for part of their range (viz. southern Australian waters). *Pseudodistoma oriens* is distinguished by its more robust zooids with wider bands of longitudinal muscles along each side of the posterior abdomen and vascular stolon, and the arrangement of its testis follicles in the posterior half of the posterior abdomen, its sessile larval adhesive organs, and its translucent test. Another sympatric species, *P. australe* is distinguished by its larvae, its lobed colonies and short vascular stolon.

The testis follicles branch off both sides of the vas deferens and when mature appear as a double or triple series in the posterior part of the posterior abdomen. This distinguishes the species from others with testes follicles in a single series posteriorly or bunched in the anterior part of the abdomen.

The large colonies of *P. africanum*: Millar, 1962 resemble those of the present species. However, all the specimens assigned to this South

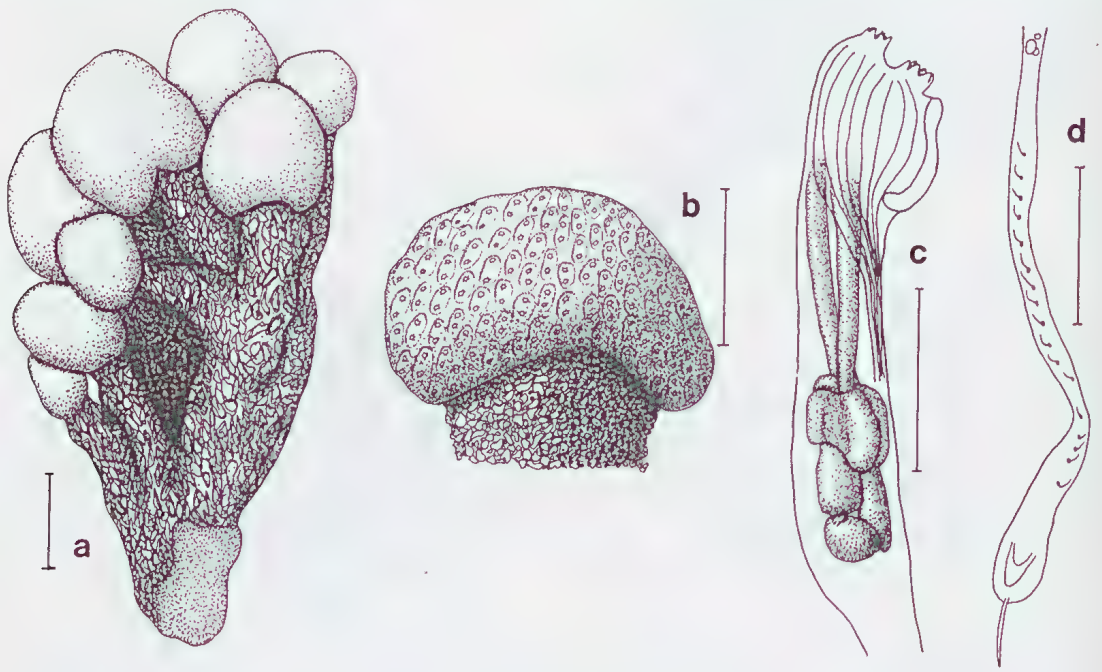


FIG. 22: *Pseudodistoma pilatum* n.sp. (paratype QM GH922) — **a**, colony; **b**, colony lobe, showing apertures (QM GH922); **c**, **d**, zooid. Scales: **a**, **b**, 1cm; **c**, 1mm; **d**, 2mm.

African species (Millar 1954, 1962) may not be conspecific. Larvae are known only for large colonies from Natal (Millar 1962), and these, although not fully developed, appear to have ampullae developing and resemble larvae of *P. candens* rather than those of the present species.

The short conical or spherical colonies from Western Australia (WAM 859.85) with sand in the basal half of the colony, but without the long tapering stalk, could be distinct, although their larvae are the same as those of the present species.

Pseudodistoma pilatum n.sp.
(Fig. 22. Plate 5b–d)

Pseudodistoma cereum: Kott 1972b, p.173 (part, not specimens from Waldegrave I < *P. oriens* n.sp.).

DISTRIBUTION

TYPE LOCALITY: South Australia (Ward I., 20–25m, coll. S.A. Shepherd 31.3.82, holotype SAM E2114 *QM GH921*, paratype QM GH922; 1–5m, paratype QM GH1296; Golden I., paratype QM GH4140; Cathedral Rock, paratype SAM E2409).

FURTHER RECORDS: South Australia (Elliston Bay — Kott 1972b SAM E2410; Nora Creina Bay SAM E2113).

DESCRIPTION

EXTERNAL APPEARANCE: The colony has solid branching, more or less cylindrical, stalks up to 1cm in diameter, and up to 2cm long, arising from a solid basal test mass. The upper free end of each stalk has a rather shallow, circular to elongate cap-like head, convex on its upper surface. In the stalk sand is present around the zooids, and the stalk and projects up into the centre of the head. The surface layer of test on the head is translucent, free of sand, and in preserved specimens contains small yellow pigment cells. Zooids open onto the upper surface of the head, each zooid with its 2 apertures close together in a small oval area. Living specimens are yellow to pink, with a sandy stalk.

INTERNAL STRUCTURE: Zooids are long, the thorax and abdomen together up to 3mm, of which the abdomen is about two-thirds. The posterior abdomen is often about 1.5cm long, with a fine sometimed forked vascular stolon from its posterior extremity. However, it is often contracted. About 20 distinct longitudinal muscles extend from the thorax to the tip of the posterior abdomen. There are about 20 stigmata in each of the 3 rows. The oesophagus is rather long, and the quadrilateral stomach is in the posterior half (rather than the middle) of the middle third of the abdomen. The small ovary is just anterior to the small male follicles which in extended zooids, are in a single series in the posterior half of the posterior abdomen although with contraction the follicles become bunched into 2 or 3 rows. A small ovary is anterior to follicles halfway down the posterior abdomen. The U-shaped heart is in the posterior tip of the posterior abdomen.

REMARKS

The species is distinguished from *Pseudodistoma acuatum* by its flat-topped (rather than pointed) lobes; the colour of the colonies ; the presence of sand in the central test; the number of stigmata per row (only 8 in *P. acuatum*). *Pseudodistoma opacum* (Brewin 1950), from New Zealand also has only 9 or 10 stigmata per row, its lobes are sessile rather than stalked, and it lacks the sand embedded in the present species.

Pseudodistoma pulvinum n.sp.
(Fig. 23. Plate 5e,f)

DISTRIBUTION

TYPE LOCALITY: South Australia (Ward I., in caves, 8m, coll. N. Holmes 12.4.83, holotype SAM E2411 *QM GH2396*, paratypes QM GH2397).

FURTHER RECORDS: South Australia (Flinders I., QM GH2300; Ward I., QM GH2423).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are sessile cushions about 1.5cm thick, fixed by most of the basal surface, and with rounded margins. The zooids open all over the more or less flattened upper surface. The test is soft and gelatinous. Living specimens are usually a translucent golden colour, although one specimen (QM GH2423) is pink. In preservative colonies are white to grey with minute black pigment cells throughout.

INTERNAL STRUCTURE: Zooids are threadlike. Extended, the thorax and abdomen are of equal length, together about 3mm long and the posterior abdomen about 1cm. One or two fine vascular processes of various lengths project from the posterior end of the zooid. About 15 longitudinal muscles extend along each side of the zooid, to the posterior end of the posterior abdomen (on each side of the heart), not extending onto the vascular processes. Sometimes the posterior abdomen is drawn up into a short, thick tapering mass behind the gut loop. Twenty-five stigmata are in the second and third rows, and at the dorsal

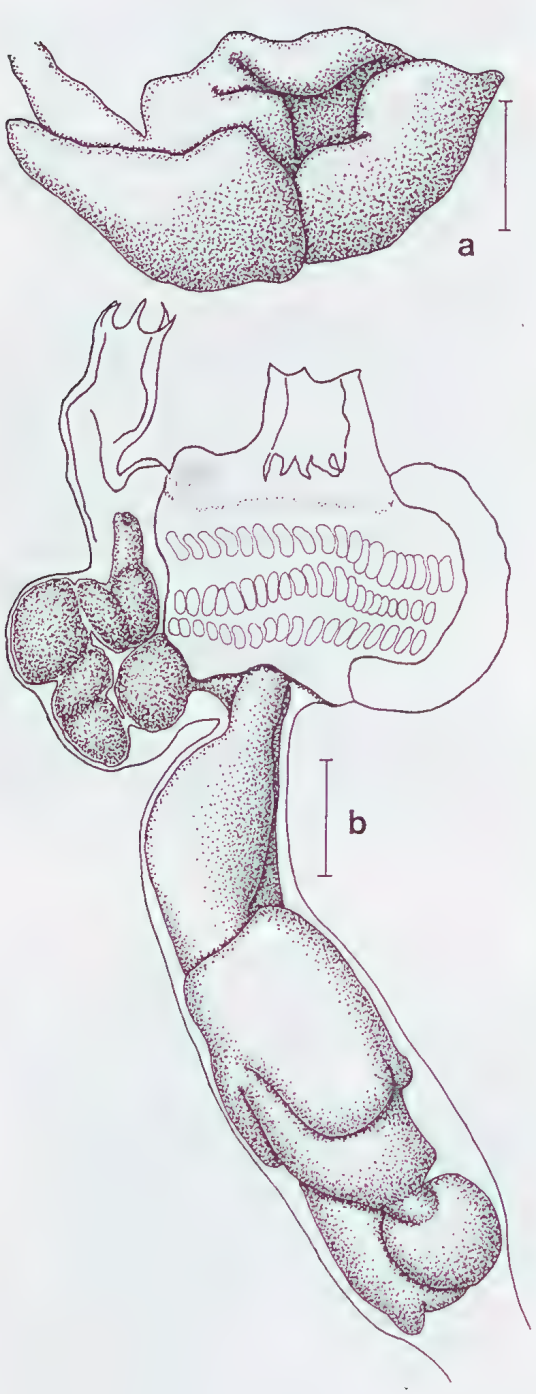


FIG. 23: *Pseudodistoma pulvinum* n.sp. — **a**, colony (QM GH2423); **b**, zooid, thorax contracted (QM GH2300). Scales: **a**, 1cm; **b**, 0.2mm.

end of the anterior row additional stigmata extend it along each side of the mid-dorsal line. The oesophagus is short, the stomach is halfway down the short abdomen, the duodenal area is relatively long, and an oval posterior stomach is in the pole of the gut loop. The rectal valve is conspicuous. A small ovary is present halfway down the posterior abdomen (see QM GH2300), but testis follicles have not been detected in any of the examined specimens.

REMARKS

The test is firmer than that of *Pseudodistoma gracilum*, the colonies are smaller, and their appearance in life with their golden translucent and slightly iridescent test is different. The dark pigment cells in the preserved material also helps to distinguish them.

Genus **Anadistoma** n.gen.

Type species: *Anadistoma attenuatum* n.sp.

The genus is erected to accommodate species with 3 rows of stigmata, transverse thoracic muscles as well as longitudinal ones, a smooth stomach, a long oesophagus with the stomach more than three-quarters of the distance down the abdomen, and gonads in the posterior abdomen. These muscular zooids with their long oesophageal neck suggest a relationship with the genus *Eudistoma* (Polycitoridae) rather than *Sigillina* (Holozoidae; see Kott 1985). The possession of these eudistomid characters together with the relatively large zooids, may mean that the relationship of this genus with *Pseudodistoma* is not as close as the presence of 3 rows of stigmata and the position of gonads in the posterior abdomen suggest.

It is unfortunate that only one specimen lot of this monotypic genus is available, and that it has no larvae which could help to confirm its relationships.

Anadistoma attenuatum n.sp.
(Fig. 24)

Pseudodistoma cereum: Kott, 1963, p.77.

DISTRIBUTION

TYPE LOCALITY: New South Wales (Montague South, near Eden, 94m, coll. CSIRO cruise CC/34 1938C, holotype AM Y1315, paratypes AM Y2212).

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: The living colonies appear to have been spherical up to 5cm in diameter. The lower half is impregnated with sand, which becomes more sparse toward the upper surface. Sand is absent from the upper part of the colony, where the test is very soft and delicate. The zooids open around the upper half of the colony and converge toward the centre of the base.

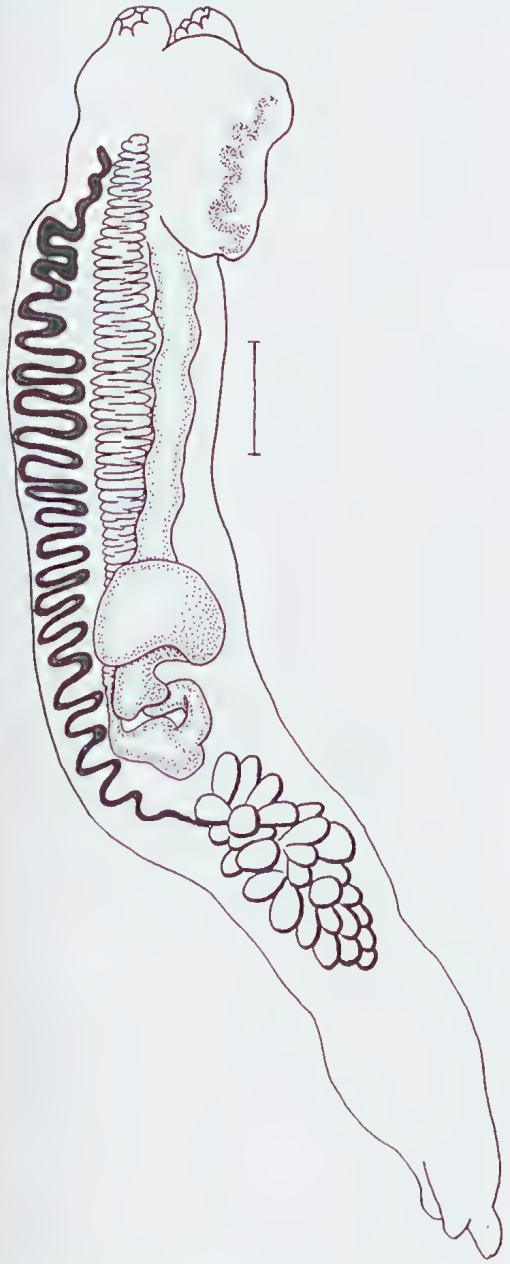


FIG. 24: *Anadistoma attenuatum* n.gen. n.sp. (holotype AM Y1315) — contracted zooid showing bunched male follicles. Scale: 0.5mm.

INTERNAL STRUCTURE: The zooids are large, and robust, up to 1cm even when contracted, and probably about 3 times that length in extended condition. The thorax and abdomen together are at least two-thirds of the total length of the zooids. The vascular stolons are very short. Both siphons are well developed with distinct lobes around the apertures and sphincter muscles. The 20 strong longitudinal muscles on the thorax extend in wide bands along each side of the abdomen and posterior abdomen. Beneath the longitudinal muscles on the thorax is an almost continuous coat of about 50 horizontal, circular muscles. About 25 long, narrow stigmata are in the second and third rows. The first row of stigmata has more perforations, and is longer, extending forward along each side of the mid-line at its dorsal end. The oesophagus is long and wrinkled in these contracted specimens. The relatively large smooth-walled stomach is in the posterior fifth or sixth of the abdomen. A wide duodenal region, and a narrow mid intestine are at the end of the descending limb of the gut loop, and an oval posterior stomach is in its pole. A rectal valve is at the proximal end of the ascending limb of the gut loop. The rectum, convoluted and pleated in these specimens, accompanies the vas deferens and the oesophagus up the long oesophageal neck to about halfway up the pharynx.

Gonads are in the anterior half of the posterior abdomen, the large, pyriform male follicles crowded together, around a small ovary.

REMARKS

There is no other taxon that displays the unique combination of characters that distinguish this monotypic species from the genus *Pseudodistoma*. It is the only species of the family in which the abdomen and thorax together are longer than the posterior abdomen.

Family POLYCLINIDAE Milne Edwards, 1842 *emend.*

The family (type genus *Polyclinum* Savigny, 1816) originally was established for genera with the gonads in a posterior abdomen. In the present more restricted sense, the family is further defined by the presence of cloacal systems, new families being erected to accommodate the genera with separately opening atrial apertures formerly comprising the subfamily Euherdmaniinae (see above).

Polyclinidae Milne Edwards, 1842 has priority over Synoicidae Hartmeyer, 1908 (type genus *Synoicum* Phipps, 1774) which Hartmeyer erroneously had proposed as the senior synonym because *Synoicum* was the earliest described genus of the family.

In the family Polyclinidae, the branchial aperture has a regularly lobed rim, but the atrial aperture is not lobed. The latter opens into the common cloaca, guided by an anterior lip that either is a projection from the body wall anterior to the opening, or is produced from the anterior border of the opening. Minute branchial papillae that may be relicts of internal longitudinal vessels are present in one genus only (*Polyclinum*). The oesophagus is short, with the stomach halfway down the abdomen. Gonads are in the posterior abdomen. These consist of a small ovary and numerous male follicles, either bunched or in longitudinal series. Larvae are small (the trunk usually less than 1mm). They have an otolith and ocellus, 3 small median adhesive organs, ectodermal ampullae and vesicles. Fertilisation is in the atrial cavity and incubation is either in the atrial cavity, or in a thoracic brood pouch constricted from the body wall.

In the Ascidiacea prolific replication results in fast growth rates and rapid responses to environmental pressures, large sized colonies, strengthening of the test allowing for greater diversity in shape than would otherwise be possible, and a high level of colony integration, organisation and the evolution of cloacal systems.

Evolutionary experiments with colonial systems occur in Polyzoinae (Stolidobranchia), and in Polycitoridae, Ritterellidae and Pseudodistomidae (Aplousobranchia), but only in exceptional cases (*Exostoma* and *Hypodistoma* see Kott 1990) are cloacal systems developed in these taxa. Nevertheless cloacal systems have evolved in a number of lineages in the Ascidiacea, viz. in some Holozoidae and all Polyclinidae and Didemnidae (in Aplousobranchia), and all Botryllinae (in Stolidobranchia).

In all these taxa the replicative process is prolific. However Polyclinidae may have particular advantages (possibly shared with Didemnidae) in flexibility and colony size and form that derive from the strength of the test, the amount of test in relation to zooid size and the use of embedded sand and other material to strengthen it. Some of the largest ascidians and the greatest diversity in shape and form of colonies occurs in this family (e.g. the three-dimensional reticulum of *Aplidium acroporum* n.sp., the large vertical buttresses of *Aplidium arboratum*. As well as extensive investing sheets and upright branched, lobed and convoluted colonies). Morphological structures of the test, independent of the overall colony habit, also occur to moderate interactions with the environment, and to insulate and protect the zooids and their apertures and enhance the advantages of the cloacal systems. Examples of this may be seen in *Synoicum castellatum* n.sp., *Aplidium craterif-erum*, and *A. lobatum* colonies with surface ridges and depressions (that protect the incurrent apertures), and upstanding cloacal apertures (that elevate the excurrent water high above the rest of the colony). It may be these morphological characteristics of the colony that have enabled Polyclinidae to adapt to a wide diversity of habitats resulting in the remarkable radiation of genera, especially *Aplidium*.

The relationships of most genera of Polyclinidae (*Polyclinum*, *Aplidiopsis*, *Sidneioides*) appear to be with Protopolyclinidae through *Polyclinum*. Branchial papillae, such as those in *Polyclinum* occur in *Monniotus*, and the stomach is similarly inclined and dorsally shorted. A curved oesophagus, smooth and obliquely or horizontally oriented stomach such as those found in *Polyclinum* are also in Holozoidae, but the larvae and the branchial sacs of Holozoidae are completely different.

However, Ritterellidae also has a claim to a close phylogenetic relationship with some (but not all) species of *Polyclinum*, *Aplidiopsis*, *Sidneioides*, and *Synoicum*, through the presence of a median dorsal papilla which protrudes from the body wall just posterior to the atrial siphon as in *Ritterella compacta*. Certain *Ritterella* species (e.g. *R. compacta*, *R. cornuta*, *R. multistigmata*, and *R. papillata*) also have papillae on the transverse branchial vessels as in *Polyclinum*. *Aplidium* with its vertical barrel-shaped and longitudinally folded stomach also may be related to the Ritterellidae.

Thus, it is possible that even the newly defined family Polyclinidae is polyphyletic, the evolution of cloacal cavities proceeding in parallel in several evolutionary lines, viz. from both Protopolyclinidae and Ritterellidae. Convergence, rather than a phylogenetic relationship, may also be the reason for similarities in the cloacal cavities and atrial apertures of many species of *Synoicum* (e.g. *S. suarenum* n.sp.) and those in the *angolanum* species group of *Eudistoma* (Polycitoridae; see Kott 1990).

The 6 genera of the family Polyclinidae are *Polyclinum*, *Aplidiopsis*, *Synoicum*, *Sidneioides*,

Aplidium and *Morchellium*. The last 2 are separated from the others by their vertical barrel-shaped stomachs, which in *Aplidium* have a longitudinally folded wall. *Morchellium* has a mulberry-like stomach and 8 branchial lobes. Eight branchial lobes also occur in some species of *Aplidium* that were formerly assigned to the genus *Sidnyum*, which here is regarded as a synonym of *Aplidium*. Branchial papillae are present only in *Polyclinum*. The position of the ovary (in the thorax) distinguishes *Sidneioides* from the other genera. *Polyclinum*, *Aplidiopsis* and *Sidneioides* are distinguished from the other genera by a constriction between abdomen and posterior abdomen. Embryos are known to develop in a brood pouch in some species of *Polyclinum*, *Synoicum* and *Aplidium*. The brood pouch (when it occurs) of the former is at mid-thoracic level, while that of the last 2 is at the postero-dorsal corner of the thorax.

The differences between *Polyclinum* and *Aplidiopsis* are often obscured. There is a particular problem in assigning those species of *Polyclinum* in which the branchial papillae are ephemeral (e.g. *P. vasculosum*). In *Polyclinum* the longitudinal muscles do not continue past the thorax to form ventral abdominal and posterior abdominal bands as they do in some species of *Aplidiopsis*, but there also are species of *Aplidiopsis* with longitudinal muscles present only on the anterior part of the zooid. The small usually horizontal, and twisted gut loop of *Polyclinum* as opposed to the large vertical one of *Aplidiopsis*, is the only reliable difference, but sometimes it is difficult to interpret.

The larvae of *Aplidium* differ from those of the other genera in that they have ectodermal vesicles that separate directly from the larval ectoderm around the anterior end of the trunk. In all the other genera the ectodermal vesicles branch off a dorsal and a ventral pair of tissue strands that trail posteriorly through the larval test, one strand on each side of the dorsal and ventral mid-lines, respectively.

Aplidium is the most diverse of the genera, and is common in tropical and temperate waters of all the oceans. *Synoicum* is moderately diverse and commonly encountered in Australian waters. Both *Aplidiopsis* and *Polyclinum* are cosmopolitan. *Polyclinum* contains species with wide geographical ranges, but *Aplidiopsis* and *Morchellium* species are seldom recorded and most are known from restricted locations in temperate waters (see below). *Sidneioides* is known only from two species, one from Japanese and the other from Australian waters.

Key to genera of Polyclinidae

1. Stomach wall longitudinally folded .. *Aplidium*
   Stomach wall not longitudinally folded 2
2. Branchial lobes 8 ..... *Morchellium*
   Branchial lobes 6 3
3. Ovary in the thorax ..... *Sidneioides*
   Ovary not in the thorax 4
4. Constriction present between abdomen and posterior abdomen 5
   Constriction not present between abdomen and posterior abdomen ..... *Synoicum*
5. Gut loop voluminous, not twisted and always vertical; branchial papillae never present ..... *Aplidiopsis*
   Gut loop small, twisted and usually horizontal; branchial papillae usually present ..... *Polyclinum*

Genus **Polyclinum** Savigny, 1816

Type species: *Polyclinum constellatum* Savigny, 1816

The test is usually soft in preservative. Sand, though embedded in the surface layer in some species, is seldom present internally. The atrial lip is often long and muscular. It usually arises separately from the body wall anterior to the anteriorly directed opening which has a distinct sphincter muscle. However, in some species the lip is produced from the anterior rim of the aperture. The body musculature consists of fine longitudinal bands that fade out on the posterior half of the thorax and do not extend onto the abdomen and posterior abdomen. Transverse muscle bands are in the transverse branchial vessels between the rows of stigmata, but no other transverse muscles are present. Branchial papillae are present on the transverse vessels, although in a few species they are present only in juvenile zooids. The thorax is always longer than the abdomen, usually with from 10 to 20 rows of stigmata, and the atrial cavity is relatively large. The oesophagus curves ventrally to enter the smooth-walled stomach along its short dorsal margin. The whole gut loop is bent horizontally from the oesophagus, and at the same time twisted so that the descending limb

is anterior (or ventral) and the ascending limb posterior (or dorsal). The distal tip of the loop is also curved to the left and dorsally. The stomach is small and smooth-walled.

The gonads are in a sac-like posterior abdomen constricted off from the abdomen by a narrow neck. The vas deferens has a complicated course, joining the abdomen in the concavity on the left side of the centre of the pole of the gut loop. It then curves around the ventral border of the descending limb of the gut loop (the mid-intestine) and continues around on the right side of the gut, following its bend at the pole before extending anteriorly on the inside of the rectum to the atrial cavity. The male opening is at about mid-thoracic level near the bilabiate anus. The small ovary is usually surrounded by male follicles. The course of the oviduct has not been determined.

In many species there is degree of polymorphism in the shape of the posterior abdomen which is related to the reproductive condition of the zooid. In zooids reproducing sexually it is short and sac-like, joined to the left side of the gut loop by a narrow neck. It contains bunched testis follicles, a small ovary, and (in the posterior end) the V-shaped heart. In zooids in the vegetative phase the posterior abdomen is long and strap-like. It is horizontally divided into buds that develop into replicated zooids. These long posterior abdomina often occur on zooids around the outer margin of colonies where growth is taking place, while in other parts of the same colony the posterior abdomina are short sacs. One or 2 moderately long, narrow vascular stolons extend out into the test behind the posterior abdomen.

Embryos are incubated either in the peribranchial cavity, or in a brood pouch constricted off from it at mid-thoracic level, near the anus. Larvae are small (the trunk length usually 0.6mm or less — only *P. glabrum* has a trunk more than 1mm long). They are unusually conservative throughout the genus, with 4 pairs of lateral ampullae, usually 4 median ampullae alternating with the 3 median adhesive organs, and clusters of epidermal vesicles along each side of the dorsal and ventral mid-lines. On each side, the dorsal vesicles are on terminal branches of a long strand of epidermal tissue extending back through the test from a point near the dorsal ampulla. Clusters of vesicles on each side of the trunk near the base of the tail are on the terminal branches of similar strands extending posteriorly on each side of the mid-ventral line, from about halfway along the ventral surface. Columnar epidermal cells form a cap on the tip of the ampullae, and sometimes on the outer wall of the epidermal vesicles (see *P. vasculosum*). The adhesive organs in this genus have long, narrow stalks and shallow epidermal cups and axial cones.

The branchial papillae are said to be the relicts of the papillae that support internal longitudinal vessels in the Cionidae, Diazonidae, and Phlebobranchia. Sometimes they are present in the younger zooids of a species but are not present in the larger, older ones (see *P. vasculosum* below).

Systems are either large with complex branching canals or they are simple and circular. Generally in this genus, sand (when it is present) is either embedded throughout the test, or it forms a sandy coating in the surface layer of test completely enveloping the colony. Naked areas on the upper surface over the zooid systems, such as occur in many *Aplidium* species, are known only in a few species (e.g. *P. festum* Hartmeyer, 1905 from Mauritius and *P. solum* nom.nov.).

Problems in defining the species of this genus result from a high degree of intrageneric conservatism in both larval and zooid morphology, as well as changes that occur with growth such as polymorphism in the posterior abdomen and changes (e.g. loss of papillae) in the branchial sac. The present studies suggest that wrong assignation of specimens on the basis of zooid similarities has resulted in apparent intraspecific variability in the presence of sand in the colony. The presence or absence of sand, and the form of the systems, together with the number of rows of stigmata and the number per row, and occasionally the shape of the posterior abdomen, constitute the principal means of distinguishing species.

The colonies of species of this genus often grow large, forming gelatinous masses up to 20cm long, and this may also contribute to confusion in species definitions.

Species of *Polyclinum* usually have a wide geographic range. The genus is well represented in Australia being especially diverse in temperate waters where there are some common indigenous species (Table 5).

Key to species of *Polyclinum* recorded from Australia

1. Sand embedded in surface test 2
   Sand not embedded in surface test 10

2. Branchial sac wide with 18 or more stigmata per row 3
   Branchial sac narrow with fewer than 18 stigmata per row 5

3. Stigmata in more than 15 rows 4
Stigmata in not more than 15 rows .... *P. saturnium*

4. Zooids in a single circular system per colony lobe; brood pouch not present .... *P. orbitum* n.sp.
Zooids not in a single circular system per colony lobe; brood pouch present ..... *P. tsutsuii*

5. Atrial lip from upper border of the aperture. 6
Atrial lip from body wall anterior to the aperture 7

6. Colony with thin keel-like base .... *P. terranum* n.sp.
Colony without thin keel-like base .... *P. tenuatum* n.sp.

7. Systems conspicuously circular .... *P. incrustatum*
Systems not conspicuously circular 8

8. Stigmata up to 17 per row; with brood pouch .... *P. marsupiale*
Stigmata up to 12 per row; without brood pouch 9

9. Stigmata in 14 or more rows .... *P. solum* nom. nov.
Stigmata in fewer than 14 rows ..... *P. fungosum*

10. Atrial lip from upper border of the opening ..... *P. nudum* n.sp.
Atrial lip from the body wall anterior to the opening 11

11. Living colonies with translucent test; branchial papillae present ..... *P. glabrum*
Living colonies with opaque test; branchial papillae not present ..... *P. vasculosum*

Species recorded from waters adjacent to Australia

Polyclinum circulatum Sluiter, 1909 from Indonesia is a flat, circular plate, sometimes with a short stalk. Three to 5 circular systems, each with 5 to 8 zooids are in each colony. Zooids have about 10 rows of 10 stigmata. Branchial papillae are not recorded. Stalks sometimes have sand but heads are naked.

Polyclinum complanatum Herdman, 1899 (> *P. depressum* Herdman, 1899) appears not properly assigned. It has a long abdomen distinguishing it from genera of Polyclinidae. It is said to have incubatory pouches packed with embryos (Herdman, 1899). It could be a species of *Pseudodistoma*, no other known genus having a brood pouch as well as both a long abdomen and a posterior abdomen, although brood pouches of *Pseudodistoma* cannot be said to be 'packed with embryos'. The number of rows of stigmata is not known.

Polyclinum constellatum Savigny, 1816 from Mauritius, has flat-topped colonies attached by a small part of the basal surface. They are without sand, and have branching double rows of zooids radiating from circular common cloacal apertures. *Polyclinum festum*: Kott and Goodbody, 1982, from Hong Kong, with large potato-shaped colonies, blue-green when living, and crowded stellate systems of zooids, may be a synonym of *P. constellatum*. The loaf-like *P. constellatum*; Michaelsen, 1923 from Hong Kong and other specimens from Hong Kong, Mozambique and St. Helena, all with radiating rows of zooids are probably also conspecific with *P. constellatum*, as Michaelsen (1923) thought them to be. The branchial sacs are relatively wide with 18 to 22 (16 to 18: Kott and Goodbody 1982) stigmata. Small papillae are present on the transverse vessels. Further probably conspecific populations are from the Atlantic (Florida, the West Indies and possibly south to Rio de Janiero), and the West Indian Ocean to Ceylon (Michaelsen 1923).

Polyclinum constellatum: Tokioka, 1967 has indistinct systems. Although the zooids, like those of *P. constellatum*, have 14 to 18 rows of stigmata with 15 to 20 stigmata per row (more in specimens from the Palau Is), and distinct branchial papillae, the sandy coating on all Tokioka's examined specimens suggests they are not *P. constellatum*.

Polyclinum crater Sluiter, 1909 has simple circular systems, each with the branchial apertures surrounding a central cloacal aperture in a surface depression. The body wall has strong muscles. About 9 rows of 6 to 8 stigmata are present. The outer surface of the test is smooth and slippery.

Polyclinum festum Hartmeyer, 1905 (see also Millar 1975) from Mauritius has flat-topped colonies with circular systems. Sand is present externally (around the base and outer border, and sometimes along radii across the upper surface) as in *Aplidiopsis amoyensis* and related species (see below).

Polyclinum hospitale Sluiter, 1895, from Thursday I. is smooth on the upper surface, with debris and sand on the under surface. Sluiter did not see either cloacal openings or systems, but both are likely to be present — the atrial opening having the usual pointed lip associated with a cloacal system. The body wall is muscular — an unusual condition for *Polyclinum*. The gut loop (including the oesophagus) is shorter than usual for this genus, and is not twisted. There are no branchial papillae. It is probable that the colony is an *Aplidium* species.

Polyclinum gelidus (Monniot, 1987) from New Caledonia, with a brownish-yellow colony resembles *P. vasculosum*, having no branchial papillae. Monniot (1987) assigned the species to the genus *Aplidiopsis*,

TABLE 5. Summary of characters of species of *Polyclinum* recorded from Australia

Species	Biogeographic range[1]	Range anticlockwise around Australia	Surface	Systems	Atrial lip[2]	Stigmata: no. rows; max no./row	Branchial papillae	Larval trunk median length (mm)	Other
P. solum. nom. nov	WP,tr	Hervey Bay. to Heron I	sandy	circular to double rows	S	14–18;14	none	—	long, posterior abdomen
P. fungosum	A,te	Bass Strait to NSW	"	"	"	12–13;14	small, pointed	0.55	
P. incrustatum	A,te	South Australia	"	"	"	15;14	"	0.6	
P. saturnium	IWP,tr	Heron I.	"	"	"	8–12;20	"	0.45	
P. marsupiale	A,te	South Australia, Tasmania	"	"	"	16–13;17	tongue-shaped	0.5	brood pouch
P. tsutsuii	WP,tr	NW Australia	"	circular	"	14–16;20	"	0.5	"
P. terranum	A,te	Cockburn Sd	"	"	R	16;15	pointed	0.7	"
P. tenuatum n.sp.	A,te	Southern Australia	"	"	"	13;12	"	—	sand relatively sparse
P. orbitum n.sp.	A,te	Bass Strait	"	"	"	18–20;24	"	0.45	1 system/lobe
P. nudum n.sp.	A,te	Coffs Harbour	naked	circular to double row	"	14–16;18	shallow rounded	0.5	soft, gelatinous test
P. glabrum	WP,tr	Heron I. to Lizard I.	"	branched	S	12–13;19	"	1.2	"
P.vasculosum	P,tr	Bass Strait	"	"		12–14;16	none	0.55	firm, gelatinous test

[1] A, indigenous; P, Pacific ocean; WP, Western Pacific; IWP, Indo-West Pacific; te, temperate, tr, tropical. [2] S, separate from rim of aperture; R, part of rim of aperture.

however its abdomen is characteristic of the genus *Polyclinum*.

? *Polyclinum nigrum* Herdman, 1906, from Sri Lanka, has a smooth shiny surface, and circular depressions in the surface, which may have contained zooids, although these are not present. There is no evidence of the genus of this colony.
The type specimen of this species from Port Jackson (AM U33, *Polyclinum nigrum* Herdman, 1899) and another (MV F59436) from the same locality have been re-examined and found to be *Sigillina* (see *S. nigra*: Kott 1990). The zooids are contracted, possibly causing Herdman to misinterpret the length of the oesophagus.

Polyclinum sundaicum (Sluiter, 1909), from the western Pacific (Fiji, Indonesia and Hong Kong: see Kott 1981, Kott and Goodbody 1982) are small stalked or sessile sandy colonies each containing one or more circular systems. They are distinguished from *P. fungosum* and *P. solum* nom. nov. by their large branchial papillae.

Polyclinum tralatica Sluiter, 1913 from Aru I. is an irregularly lobed, cylindrical, gelatinous mass along a bryozoan or gorgonian stalk. Its outer surface grey with a pale violet hue. The body wall is moderately muscular. The species resembles *P. vasculosum* in the absence of branchial papillae and in its 10 rows of about 10 to 12 stigmata

Polyclinum fungosum Herdman, 1886
(Fig. 25)

Polyclinum fungosum Herdman, 1886, p.190.
Polyclinum marsupiale: Kott, 1976, p.60.
Synoicum hypurgon: Kott, 1976, p.62.

DISTRIBUTION
NEW RECORD: Victoria (Bass Strait, QM G12748).
PREVIOUSLY RECORDED: Victoria (Westernport — MV F59365 F59431–2 Kott 1976). New South Wales (Port Jackson — Herdman 1886).

DESCRIPTION
EXTERNAL APPEARANCE: The small (about 5mm diameter) newly recorded specimen from Bass Strait is mutilated, possibly stalked, mushroom-shaped, with a firm, translucent test, an external layer of sand, and some sand internally. The zooids are crowded, obscuring the form of the systems. Larger (to 4cm diameter) colonies (MV F59431) are soft, mushroom-shaped, fixed by a small part of base or with a small stalk. In preservative they are collapsed, with a wrinkled, furrowed surface. Sand encrusts the sides and under surface, is in patches on the upper surface, and is sparse internally.

INTERNAL STRUCTURE: Zooids are about 3 to 4mm long, with a narrow thorax, small horizontal

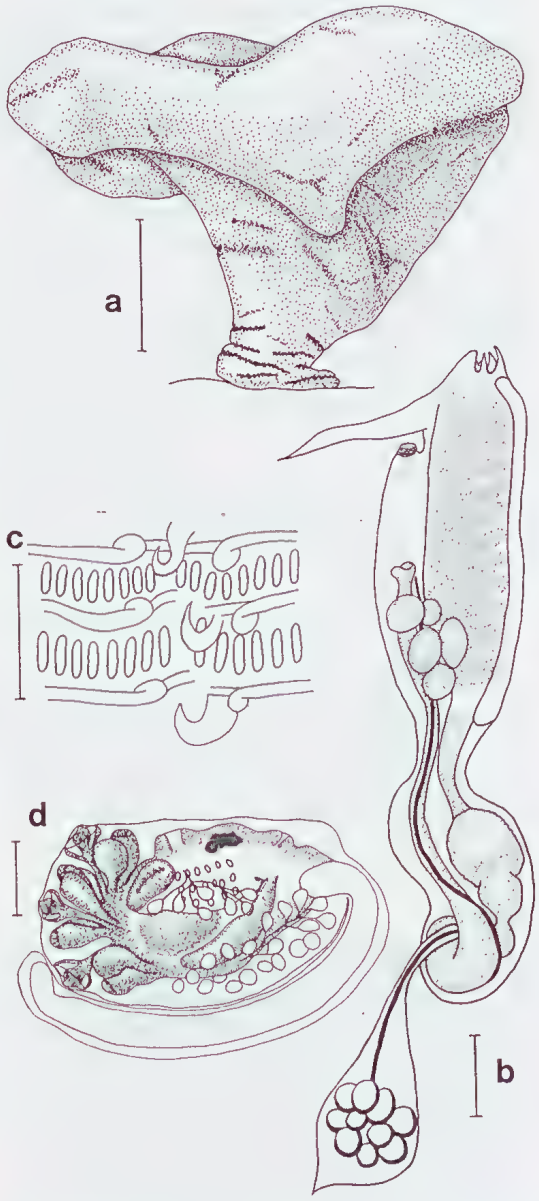


FIG. 25: *Polyclinum fungosum* — **a**, colony (MV F59431); **b**, zooid with embryos in atrial cavity (MV F59431); **c**, dorsal part of portion of branchial sac showing kink in transverse vessels (MV F59431); **d**, larva (QM G12748). Scales: **a**, 1cm; **b**, 0.5mm; **c**, 0.2mm; **d**, 0.1mm.

gut loop, and sac-like posterior abdomen. The branchial lobes are triangular and pointed, and the atrial lip is long and narrow. Six to 10 fine longitudinal muscles are present on the anterior half of the thorax. Fine circular muscles are present in the transverse vessels between the rows of stigmata. The branchial sac is narrow, with 12 or 13 rows of 12 to 14 short oval stigmata. A short expansion of the transverse vessels on each side of the dorsal languets in some of the zooids could have resulted from contraction of the transverse muscle fibres in the vessels. The branchial papillae on the margin of the transverse vessels are small, shallow, triangular protrusions about one to every one and a half stigmata.

The gut forms the usual small, horizontal loop with a smooth-walled stomach, a long duodenal area and an oval posterior stomach. The sac-like posterior abdomen has a short neck and is pointed posteriorly. Male follicles are clustered behind and to the side of a relatively large ovary, which has up to 5 relatively large eggs and some small ones.

The Bass Strait specimen contains about 12 embryos in the right peribranchial cavity. Larvae have a row of median ampullae alternating with the adhesive organs and 4 lateral ampullae along each side. A ventral pair of rows of large epidermal vesicles expands into a postero-ventral cluster on each side beneath the tail. Corresponding rows are present on each side of the mid-dorsal line. The larval trunk is 0.4 to 0.5mm long, and the broad tail barely reaches its anterior end. Each of the ampullae has a terminal cap of columnar cells, although these are more conspicuous on the long, narrow median ampullae than on the rounded lateral ones.

Remarks

The type specimen of this species (Herdman 1886) is a circular, dome-shaped cushion, 1.6cm high, 3.3cm in maximum dimension. It has a hard sandy external coating. Zooids are crowded in the colony, and systems were not determined. Long, narrow stigmata are in 10 to 12 rows of about 12. Herdman did not observe any branchial papillae. The gut loop is small, with a smooth stomach, and although Herdman did not observe it to be horizontal, it has the short oesophagus and short mid-intestinal region that is characteristic of *Polyclinum*, and it also has a polyclinid, stalked, sac-like posterior abdomen with the ovary surrounded by male follicles. The species apparently is assigned to the correct genus rather than belonging to *Synoicum* as Millar (1982) suggested.

Some of the zooids of the holotype contained larvae. Although the exact number present is not recorded it appears that there were more than one or 2 and that they were in the atrial cavity, as a brood pouch is not mentioned.

The crowded zooids, the narrow thorax, the number of rows of stigmata, and the form of the colony of the holotype and the newly assigned and recorded specimens are all identical. The only point of difference is the presence of small inconspicuous branchial papillae in the Victorian specimen. Herdman may have overlooked these as they are difficult to detect.

Tropical sandy species such as *P. tsutsuii* and *P. saturnium* have broader branchial sacs with more stigmata per row. *Polyclinum incrustatum* n.sp. is distinguished from the present species by its slightly more stigmata per row (14) and more rows (15), and by its large tongue-like branchial papillae. The sympatric *P. marsupiale* also has larger branchial papillae, more rows of stigmata and more stigmata per row, and thinner more irregular colonies than the mushroom-like ones of the present species. It also has a brood pouch.

Polyclinum glabrum Sluiter, 1895
(Fig. 26)

Polyclinum glabrum Sluiter, 1895, p. 168; 1913, p. 71.

Distribution

New Records: Western Australia (Montebello Is, QM GH5507). Queensland (Capricorn Group, QM GH5038–41 GH5563; Townsville Harbour, QM GH2094; Lizard I, QM GH319 GH5024 GH5036–7 GH5042).

Previously Recorded: Indonesia (Sluiter 1895, 1913).

Description

External Appearance: The colonies from shallow reefal habitats are irregular cushions, or robust, spreading sheets, up to 1cm thick and 6cm in maximum dimension, with soft, transparent test entirely free of sand, and orange zooids. Collector's notes describe them as 'soft orange' and 'chinese orange' (Ridgeway 1886). In preservative these colonies are transparent and yellowish to a translucent, soft grey or beige colour. Common cloacal apertures are relatively crowded, especially around the borders of the colony. Some protrude from the surface on conical prominences, but others are sessile, irregular and extensive openings. Atrial lips of zooids are

in the test around the rim of the cloacal openings. In some preserved zooids, the tips of the atrial lips contain dark pigment. Cloacal systems are crowded, and zooids also are crowded along each side of the canals that radiate from the cloacal apertures.

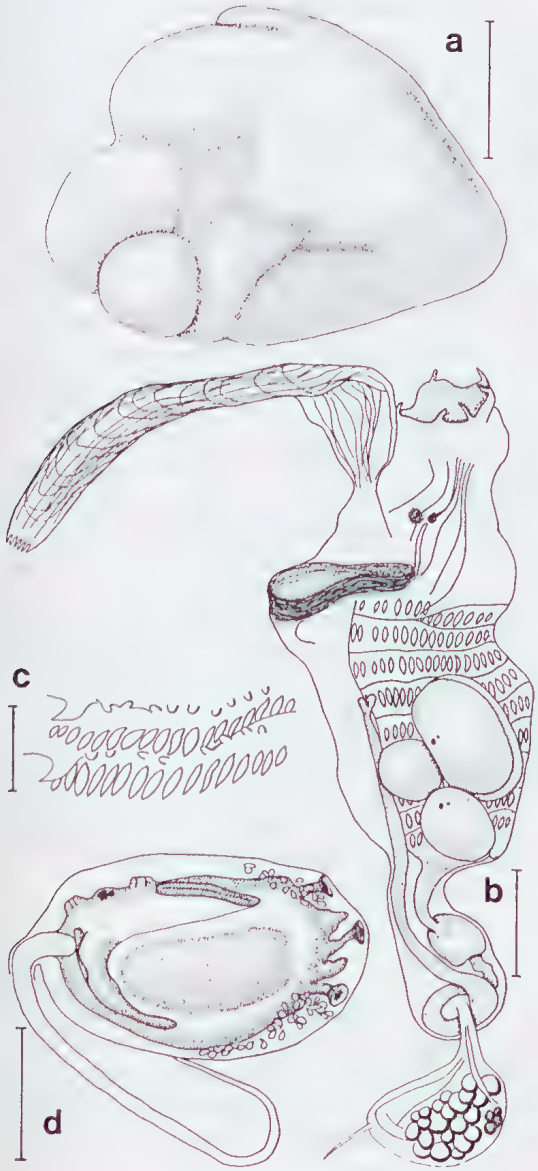


FIG. 26: *Polyclinum glabrum* — **a**, colony (QM GH319); **b**, zooid relaxed with embryos in atrial cavity, anterior rows of stigmata obscured (QM GH319); **c**, portion of branchial sac showing dorsal languets and branchial papillae on the transverse vessels (QM GH319); **d**, larva (QM GH5563). Scales: **a**, 2cm; **b**, 0.5mm; **c**, 0.2mm; **d**, 0.4mm.

The colony from the Montebello Is is a large (maximum dimension 4cm) flattened slab which, with a light coating of sand on one side, appears to have been lying on its side when collected. Originally it probably stood upright, attached to pebbles by its narrow base. Systems open on both sides of the colony, which has an irregularly subdivided surface.

INTERNAL STRUCTURE: The zooids are about 4mm long, with a large thorax, a small horizontal gut loop, and a spherical to tapering (QM GH2094) posterior abdomen. The atrial lip is long and moderately broad, and contains fine longitudinal muscles. It extends along the roof of the cloacal canal toward the cloacal aperture and ends in a single point or a fringe of up to 6 minute papillae. A small median papilla projects from the body wall just behind the atrial aperture. Fine longitudinal muscles are present over the anterior part of the thorax. There are 12 or 13 rows of up to 19 oval stigmata with the maximum number in rows 2 to 6. Rounded branchial papillae are on the transverse vessels, about one and a half per stigma. The gut loop is small and horizontal. The posterior abdomen is attached to it by a relatively long neck. The posterior abdomen is either sac-like or (sometimes) it tapers to a short vascular stolon that projects from its posterior end behind the heart.

Three embryos are in the posterior end of the atrial cavity of specimens from the Capricorn Group collected in December, Lizard I. specimens collected in July, and 6 in those from Montebello Is collected in August. Larvae have a long (1.2mm) trunk with median and lateral ampullae anteriorly, and dorsal and ventral clusters of ectodermal vesicles along each side of the mid-line.

REMARKS

Sluiter (1895) described the type specimen as a large naked cushion, less than 1cm thick, with a smooth surface, without conspicuous systems, and with conspicuous branchial papillae. Although he believed this colony to be juvenile, both male and female gonads are present. The cloacal systems in the present specimens are so crowded that they are hard to distinguish, and in view of the similarities in the branchial sac, and the smooth-surfaced colonies without sand, they seem to be conspecific with the Indonesian species.

The irregular shape and soft consistency of the colony distinguishes it from the more regular and robust *P. constellatum*. The branchial papillae, the more numerous stigmata per row, and the

transparent test of the living specimens distinguish it from *P. vasculosum*. The larval trunk is unusually long for this genus.

Sluiter's specimen from Ambon (1895) was grey in preservative with a reddish-violet glimmer, but this does not occur in other known colonies.

Polyclinum incrustatum Michaelsen, 1930
(Fig. 27. Plate 6a,b)

Polyclinum neptunium: Michaelsen, 1930, p.542 f. incrustatum. Kott, 1963, p.83 (part, South Australian specimen).

DISTRIBUTION

NEW RECORDS: South Australia (Golden I., SAM E2145 *QM GH4185*; Hopkins I., QM GH4192; Margaret Brock Reef, SAM E2531; Perforated I., QM GH4141; The Gap, QM GH4163; Cathedral Rock, QM GH4145 GH5209; Nuyts Arch., SAM E2528). Victoria (Portland Harbour, MV 59434 F59437).

PREVIOUSLY RECORDED: Western Australia (Bunbury, Albany — Michaelsen 1930). South Australia (Reevesby I. — Kott 1963).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are thick sheets, sometimes with swellings, high convoluted ridges and irregularities on the surface. The common cloacal apertures are sessile or on small raised prominences about 5mm apart. The zooids open all around the ridges and irregularities, as well as on the flat part of the colony. Sand is present in a single layer in the surface test. Sometimes it is interrupted by the prominences raising the cloacal apertures above the surface, but in other specimens these are also covered with sand. Embedded sand is only sparse in the internal test between the zooids, but the grains are moderately crowded between the zooid systems. Cloacal cavities are small, circular, and are confined to the area beneath the cloacal aperture. The zooids are arranged around these cavities. The atrial lip of each zooid in the system extends across the roof of the cavity and is inserted into the test around the rim of the cloacal aperture. The branchial apertures open in a small surface depression surrounding each cloacal prominence.

INTERNAL STRUCTURE: Zooids are about 8mm long, with the narrow thorax about three-quarters of the total length. A small horizontally oriented gut loop has an almost spherical to long, cylindrical posterior abdomen connected to it by a short narrow neck. There is a narrow vascular stolon from the posterior end of the posterior abdomen.

The atrial lip is long and narrow. It has denticulations on its free tip. The usual muscular atrial siphon projects forward to open into the base of the cloacal cavity around its outer margin.

The anterior part of the zooid, including the branchial lobes and atrial lip, contains black pigment. Fine longitudinal muscles (about 8) extend from the branchial siphon to about halfway down the thorax. Fifteen rows of 13 or 14 longish-oval stigmata have transverse vessels with flat tongue-shaped papillae along the margin, about one to every stigma. These are delicate and hard to see without staining.

The oesophagus is short, and curved ventrally to the small, smooth-walled, horizontal stomach. The distal end of the gut loop is bent to the left. The narrow neck connecting the posterior abdomen is attached in the pole of the gut loop in the concavity of this distal bend of the loop. It appears to have been drawn up onto this side of the gut loop, as the vas deferens moves to the outer curve of loop and follows the curve of the rectum where it lies adjacent to the duodenum, stomach and oesophagus. The rectum terminates in a 2-lipped anus halfway up the branchial sac.

Up to 20 male follicles surround the ovary in the sexual posterior abdomen. The long (3mm) vegetative posterior abdomen is in colonies collected in April from Perforated I. (QM GH4141) and in February from Franklin I. (SAM E2528).

Up to 7 embryos are clumped together in the atrial cavity of zooids from Portland Harbour (MV F59434) but the collection date is not recorded. Larvae have a trunk nearly 0.6mm long, with median and lateral ampullae, and postero-ventral and antero-dorsal vesicles.

REMARKS

Zooids of this species are relatively large and that, together with their distinct circular systems helps to distinguish them from other species.

Michaelsen (1930) believed specimens from Western Australia with embedded sand throughout to be a form of *P. neptunium* Hartmeyer, 1912 for which the type locality is South Africa. Hartmeyer's species has a more or less spherical stalked head, and, with the exception of one specimen (which has sand in the lower half of the colony), is without sand either on the surface or embedded (see also Millar 1962). The abdomen is clavate when mature, and long and cylindrical when immature, the zooids are in circular to double-row systems, and have conspicuous branchial

FIG. 27: *Polyclinum incrustatum* — **a**, general view of colony (QM GH4185); **b**, close-up view of surface of colony with common cloacal apertures surrounded by branchial apertures (MV F59434); **c**, zooid in colony showing atrial lip in test above cloacal cavity, and branchial aperture amongst sand adhering to outer surface (QM GH4185); **d**, abdomen and vegetative posterior abdomen (QM GH4141); **e**, portion of branchial sac showing branchial papillae (QM GH4141). Scales: **a**, 2cm; **b**, 2mm; **c–e**, 0.5mm.

papillae. Michaelsen (1930) and Kott (1963) assigned the western and southern Australian material to this species largely on the basis of the long vegetative abdomen, which now is known to occur in other species of this genus.

Michaelsen identified 2 forms, *Polyclinum neptunium* f. typicum being the form in which sand is absent altogether or present only in the basal layer; and *P. neptunium* f. incrustatum with sand throughout. The present sessile specimens from South Australia, with moderate amounts of embedded sand between the systems, with an almost continuous layer on the surface, and with strictly circular systems and raised cloacal apertures, appear to be conspecific with *P. neptunium*: Michaelsen, 1930 f. incrustatum recorded from Bunbury and Albany, but not with the stalked South African species. The stalked specimen from Western Australia (Kott 1963), does have characters in common with the South African species, but is distinguished by the flattened upper surface. It resembles *Polyclinum circulatum* Sluiter, 1909, and may be a synonym. There is insufficient data available for the Shark Bay specimens of *P. neptunium* f. typicum (see Michaelsen 1930) with double rows systems and sand in the lower half of the colony to assign it to a species.

Polyclinum marsupiale Kott, 1963
(Fig. 28a–c. Plate 6c,d)

Polyclinum marsupiale Kott, 1963, p.83 (part, not specimen from Heron I.? < *P. saturnium*). **Not** Kott 1976, p.60 (< *P. fungosum*).

? *Polyclinum macrophyllum*: Kott, 1963, p. 82 (part, specimen from Rottnest I.).

DISTRIBUTION

NEW RECORDS: Western Australia (Albany, QM GH5059). South Australia (Kingston, QM G10138). Victoria (Deal I., QM G10175; Portland, MVF 59433).

PREVIOUSLY RECORDED: Western Australia (Rottnest I. — AM Y1330 Kott 1963). South Australia (Victor Harbour — Kott 1963); Tasmania (Hunter I. — Kott 1963).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are soft, rather irregular sheets, up to 4cm in maximum extent, investing weed; to upright structures to 1m high with vertical flattened ribs (QM G10175). The zooids are in circular systems. The branchial apertures open to the surface between the sand grains that form an otherwise continuous coat over the outer surface. Sand also is sparsely distributed in the soft, transparent internal test that forms thin partitions between the crowded zooids. Dark pigment in the anterior part of the zooid can be seen where the branchial apertures open to the surface. Common cloacal apertures protrude from the surface.

The colonies from Albany (sea grass beds) are small (less than 1cm in diameter) sessile and upright, covered with a layer of sand, and with characteristic zooids in circular systems.

INTERNAL STRUCTURE: The zooids are small, 3 to 4mm long, with a relatively large conspicuous thorax more than half the total length. Longitudinal muscles are fine and extend only over the anterior part of the thorax (about the first 3 rows of stigmata). The branchial lobes are triangular. The tongue-shaped, moderately muscular atrial lip, undivided to tridentate terminally, projects in front of the atrial aperture.

Stigmata are oval, and are in 12 or 13 rows with a maximum of 16 or 17 per row. The branchial papillae, on the transverse vessels are well-defined, tongue-shaped, and about one per stigma. The gut loop is small, horizontal with the pole of the loop curved to the left and the short neck of the posterior abdominal sac attached to the dorsal (concave) side of the gut loop.

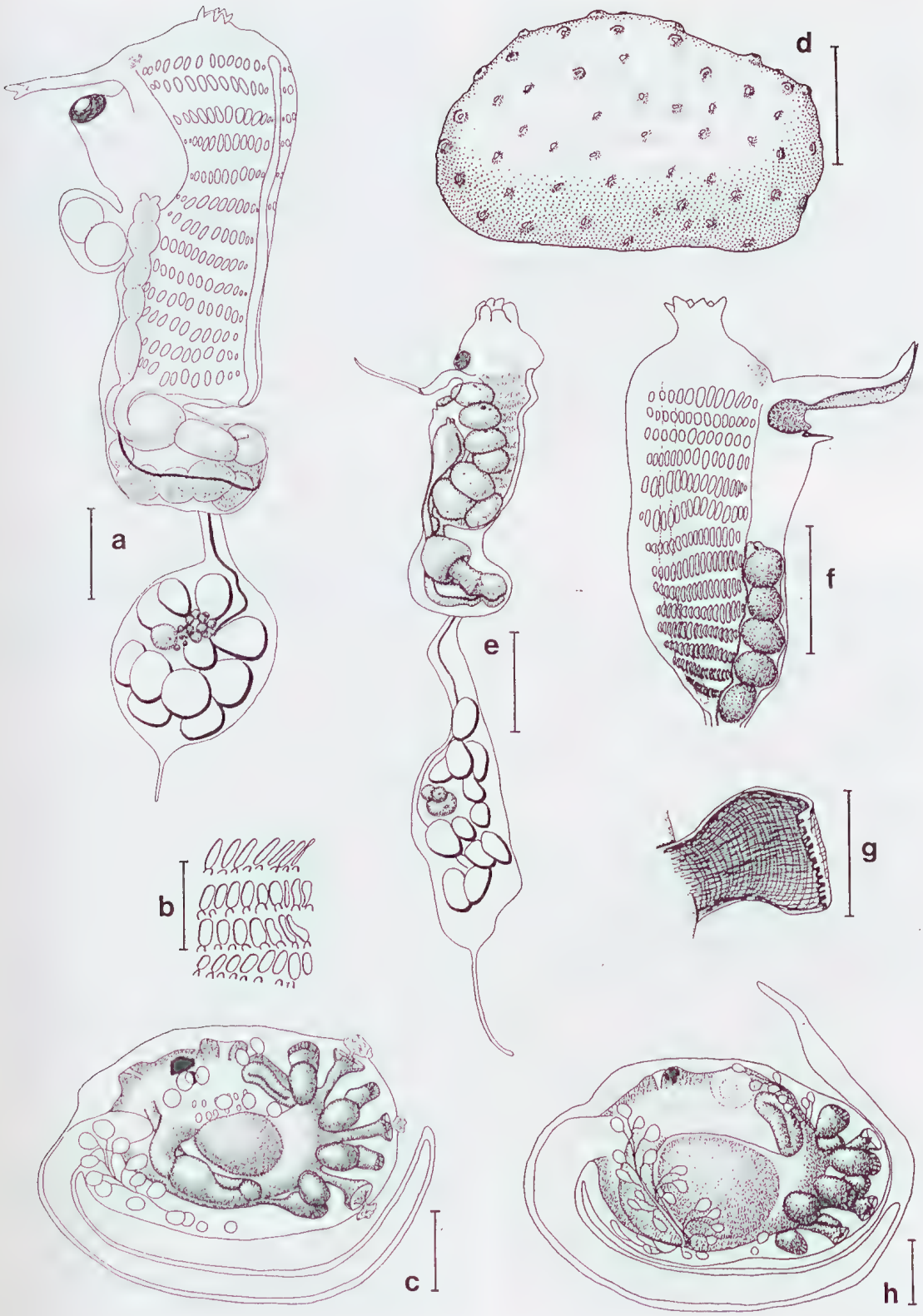
The newly recorded specimen collected in September has 2 or 3 well developed embryos in the brood pouch which projects from the thorax about halfway up the thorax (opposite the sixth row of stigmata).

The larval trunk is 0.5mm long. It has the usual median and lateral ampullae and postero-ventral and antero-dorsal bunches of numerous ectodermal vesicles. The vesicles continue anteriorly in a row along each side of the median line. The tail is wound halfway around the trunk. The caps of columnar cells are more conspicuous on the narrow median ampullae than the rounded lateral ones.

REMARKS

Polyclinum marsupiale is a temperate species,

FIG. 28: *Polyclinum marsupiale* (QM G10138) — **a**, zooid with embryos in brood pouch; **b**, branchial sac showing papillae; **c**, larva. *Polyclinum nudum* — **d**, colony (QM GH5388); **e**, zooid with embryos in atrial cavity and ovary surrounded by male follicles in posterior abdomen (QM GH5387); **f**, thorax (holotype QM GH5391); **g**, atrial lip (holotype QM GH5391); **h**, larva (holotype QM GH5391). Scales: **a**, **f**, 0.5mm; **b**, 0.25mm; **c**, 0.2mm; **d**, 2cm; **e**, **g**, 1mm; **h**, 0.1mm.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characterised by the layer of sand in the surface test, black pigment in the zooids, soft internal test, and crowded circular systems of small zooids. The tropical *P. saturnium* also has small zooids, and they have a similar pharynx with 8 to 12 rows of 18 to 20 stigmata per row. However they lack the brood pouch of the present species.

The small colony from Rottnest I. assigned to *P. macrophyllum* : Kott, 1963 is similar to the newly recorded one from Albany and may be a specimen of the present species.

Kott (1963) reported an incipient brood pouch in a specimen from Heron I. she assigned to *P. marsupiale*. This has not been confirmed, and that specimen is possibly one of *P. saturnium*.

The other temperate sandy species with dark pigment in the zooids, *P. incrustatum*, has firmer colonies, larger zooids, more conspicuous circular systems, more rows of stigmata, and fewer per row.

Polyclinum nudum n.sp.
(Fig. 28d–f. Plate 6e–g)

DISTRIBUTION

TYPE LOCALITY: New South Wales (Coffs Harbour, old jetty piles, 0.5m, coll. AIMS Bioactivity Group 18.2.88, holotype QM GH5391; 16.2.88, paratype QM GH5387.

FURTHER RECORDS: New South Wales (Coffs Harbour, QM GH5388 GH5390).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are cushion- or dome-shaped, to about 9cm in diameter and up to 1.5cm thick. The test is soft and gelatinous, translucent internally, but with an opaque layer where the anterior ends of the zooids are crowded together at right angles to the surface.

Colonies are dark, black in preservative, and black immediately after removal from the substrate. The photograph of a colony *in situ*, however, shows it to be whitish green (QM GH5387) or yellow (QM GH5388), or brownish red with yellow zooids (QM GH5390). Zooids are in irregularly branching relatively short double rows, one row along each side of canals that converge to common cloacal apertures about 5mm apart. These apertures are sometimes sessile in the preserved colonies, but in the living colony they protrude from the surface on conical elevations. Occasionally there are a few patches of sand adhering to the surface test, but most of the surface is naked, and there is no embedded sand.

INTERNAL STRUCTURE: The zooids are large, about 1cm long, of which the thorax and abdomen together are about half, and the stalked posterior abdomen the other half. Only very fine longitudinal muscles extend over the anterior part of the thorax, including an extensive prestigmatal area.

The branchial siphon is long, with large lobes around the aperture and a long, prebranchial area. The atrial tongue is long, extending out from the upper rim of a large opening. Its tip is variable, sometimes being a single point, or with up to 12 minute papillae along a straight edge. The muscles in the atrial lip form a fine, irregular meshwork. A small, median dorsal papilla is present just posterior to the atrial opening.

There are 14 to 16 rows of up to 18 relatively short, oval stigmata. Small branchial papillae (about one per stigma) are on the transverse vessels. The gut forms the usual small, horizontal loop characteristic of this genus. The vas deferens also makes the characteristic loop around the outside of the bend of the gut loop before extending around onto the other side.

The long, club-shaped posterior abdomen has a long narrow neck, joining it to the abdomen. It contains up to 24, loosely bunched, large pear-shaped male follicles. A small ovary is from one third to half the distance down the posterior abdomen, surrounded by male follicles. A long vascular stolon extends back from the tip of the posterior abdomen.

Up to 7 embryos at a time are crowded in the posterior half of the right peribranchial cavity of the holoytpe. They are progressively advanced postero-ventrally in the postero-dorsal quarter of the atrial cavity, then anteriorly and dorsally in the postero-ventral quarter.

A tailed larva has a trunk 0.5mm long, with the tail wound about three-quarters of the way around it. A large otolith and ocellus are in the atrial cavity. A lateral ampulla is on each side of each of the 3 median adhesive organs. Also there is a median dorsal and a median ventral ampulla. Patches of epidermal vesicles are antero-dorsal and postero-ventral.

REMARKS

The present species is unusual in having the atrial tongue arising from the upper rim of the atrial aperture (as in *Polyclinum orbitum* n.sp. and *P. tenuatum* n.sp.). Like *P. orbitum* n.sp., the larvae lack median ampullae.

The long club-shaped posterior abdomen is unique. It differs from that of those *Polyclinum* spp. which have a long posterior abdomen only

in the vegetative phase. The long posterior abdomen of the present species has mature sexual organs in it, and in that it resembles *P. solum* nom. nov. However, although the latter species has similar colonies, it is distinguished from the present one by its smaller zooids, relatively small posterior abdomen with fewer and smaller male follicles, fewer stigmata in each row (i.e. a narrower thorax), and its lack of branchial papillae.

The colonies resemble some more fleshy ones of *P. vasculosum*. However, the cloacal canals of the present species do not branch as much, the atrial tongue is not separate from the opening, it has branchial papillae, and it has a long posterior abdomen in its sexual phase.

Polyclinum orbitum n.sp.
(Fig. 29)

DISTRIBUTION
TYPE LOCALITY: Victoria (Ninety Mile Beach, 10 km SW Seaspray, 560 m offshore calcenarite reef, 12m depth, fast currents, coll. J.E. Watson August 1977, holotype QM G12730, paratype QM G12731).
FURTHER RECORDS: None.

DESCRIPTION
EXTERNAL APPEARANCE: Colonies are a number of trumpet-shaped lobes up to 1cm diameter at the wide, free end, and 2cm long, narrowing basally to a common stalk. The outer surface is covered with sand, but there is no sand in the soft internal test. Zooids form a single circular system of up to 8 zooids in each lobe. Branchial apertures, around the outer rim of the upper free border are directed laterally. The test is raised into a rounded swelling over the anterior end of each zooid, around the margin of the upper, free end of each lobe. A protuberant cloacal aperture is in the centre of the upper surface.

INTERNAL STRUCTURE: Zooids are up to 1cm long, of which the thorax and abdomen together comprise less than half the length. The abdomen is small, and there is a particularly long, narrow neck, about half the length of the posterior abdominal sac, attaching it to the gut loop. Thus, posterior abdomina lie in the basal common stalk of the colony.

The branchial lobes are well defined. The atrial lip is large and pointed, rising from the anterior rim of the anteriorly directed atrial aperture. Eighteen to 20 rows of stigmata each have 22 to 24 stigmata. Transverse vessels have conspicuous rounded papillae (about one to every 1.5 stigmata).

The particularly small gut loop is horizontal. The ovary is surrounded by and mixed with male follicles in the tear-drop-shaped to long fusiform posterior abdomen.

One or two embryos are in the peribranchial cavity of the type specimens. The larval trunk is 0.45mm long, and the tail is wound three-quarters of the way around it. The 3 median adhesive organs are wide and shallow with thick stalks and wide, shallow axial cones. Four lateral ampullae with enlarged ectodermal cells over the tip of each are present along each side of the adhesive organs. Median ampullae are not present. A row of ectodermal vesicles are present along each side of the mid-ventral and mid-dorsal lines, but a postero-ventral clump was not detected. The otolith is larger than usual, and in one larva 3 otoliths are present (QM G12731).

REMARKS
The species is distinguished by its simple circular systems, the shape of the colonies, the long neck connecting the posterior abdomen to the gut loop, and the large branchial sac. Millar (1977) described a similar *Polyclinum* from the Brazilian Shelf which, however, has a narrow branchial sac with only half the stigmata of the present species.

The species is unusual in having the atrial lip continuous with the anterior rim of the opening. The larvae are unusual in the genus in the absence of median ampullae, and in having fewer ectodermal vesicles than usual. These larvae are also amongst the smallest known in this genus.

The colonies resemble those of *Synoicum stewartense* (Michaelsen, 1924) from New Zealand (see Millar 1982). Generic characters, including the absence of branchial papillae, as well as its purple colour, distinguish the New Zealand species.

Polyclinum saturnium Savigny, 1816
(Fig. 30)

Polyclinum saturnium Savigny, 1816, p.190. Hartmeyer, 1915, p.424. Michaelsen, 1920, p.9. **Not** Tokioka, 1962, p.260 (< *P. tsutsuii*). **Not** Rho, 1966, p.212; 1971, p.108; 1975, p.126 (< *P. tsutsuii*).
Polyclinum vasculosum: Tokioka, 1967, p.51 (part, specimen from Baliwasan, Philippines).
Polyclinum marsupiale: Kott, 1963, p.83 (part, Heron I. specimen).

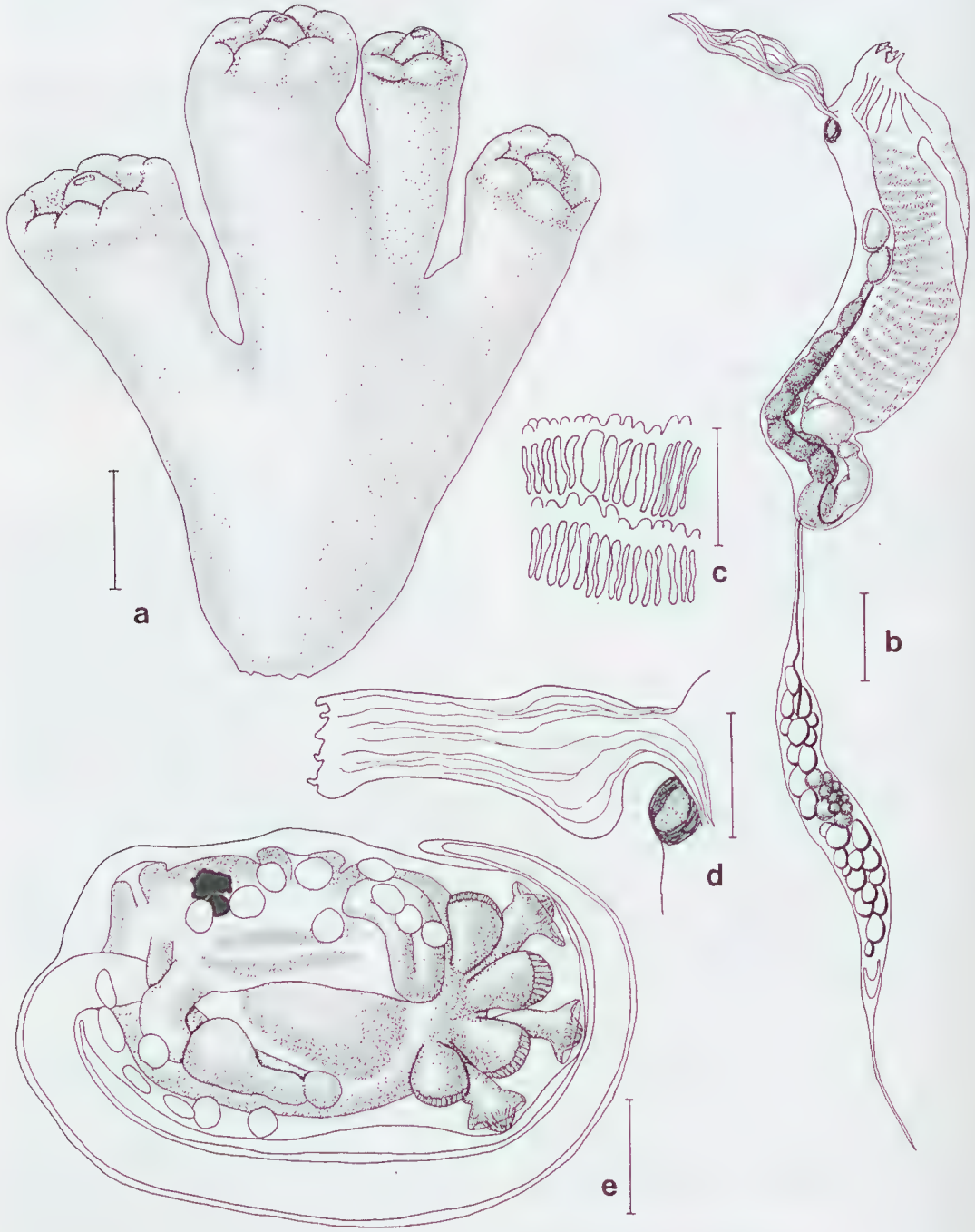


FIG. 29: *Polyclinum orbitum* n.sp. — **a**, colony (paratype QM G12731); **b**, zooid with 2 small embryos in atrial cavity (paratype QM G12731); **c**, portion of branchial sac showing branchial papillae on transverse vessels (holotype QM G12730); **d**, atrial opening with lip (holotype QM G12730); **e**, larva (paratype QM G12731). Scales: **a**, 5mm; **b**, 0.5mm; **c**, **d**, 0.25mm; **e**, 0.1mm.

? *Polyclinum tsutsuii*: Tokioka, 1967, p.47 (part, specimen from Baliwasan, Philippines).

DISTRIBUTION

NEW RECORDS: Western Australia (Dongara, WAM 280.83). Queensland (Heron I., QM GH5034–5 GH5260 GH5568).

PREVIOUSLY RECORDED: Suez, Red Sea (Savigny 1816, Hartmeyer 1915, Michaelsen 1920). Philippines (Baliwasan — USNM 11648 Tokioka 1967).

DESCRIPTION

EXTERNAL APPEARANCE: The re-examined colonies from the Philippines as well as the Heron I. colony are cushions up to 1.0cm in diameter, with a layer of sand externally. The internal test is soft and transparent. Zooids are arranged in circular systems, and the surface layer of sand is interrupted where they open to the surface. Sometimes the zooids extend along each side of short canals that radiate from the apertures to form stellate systems. The zooids are yellow in freshly preserved material with purple in the test above them. In the living specimens the zooids are 'burnt amber' or 'aster purple' and the test translucent. One juvenile colony is recorded as having bright red pigment in the zooids and the test.

INTERNAL STRUCTURE: Zooids are about 4mm long, with a moderately long neck joining the posterior abdomen to the abdomen. The atrial lip

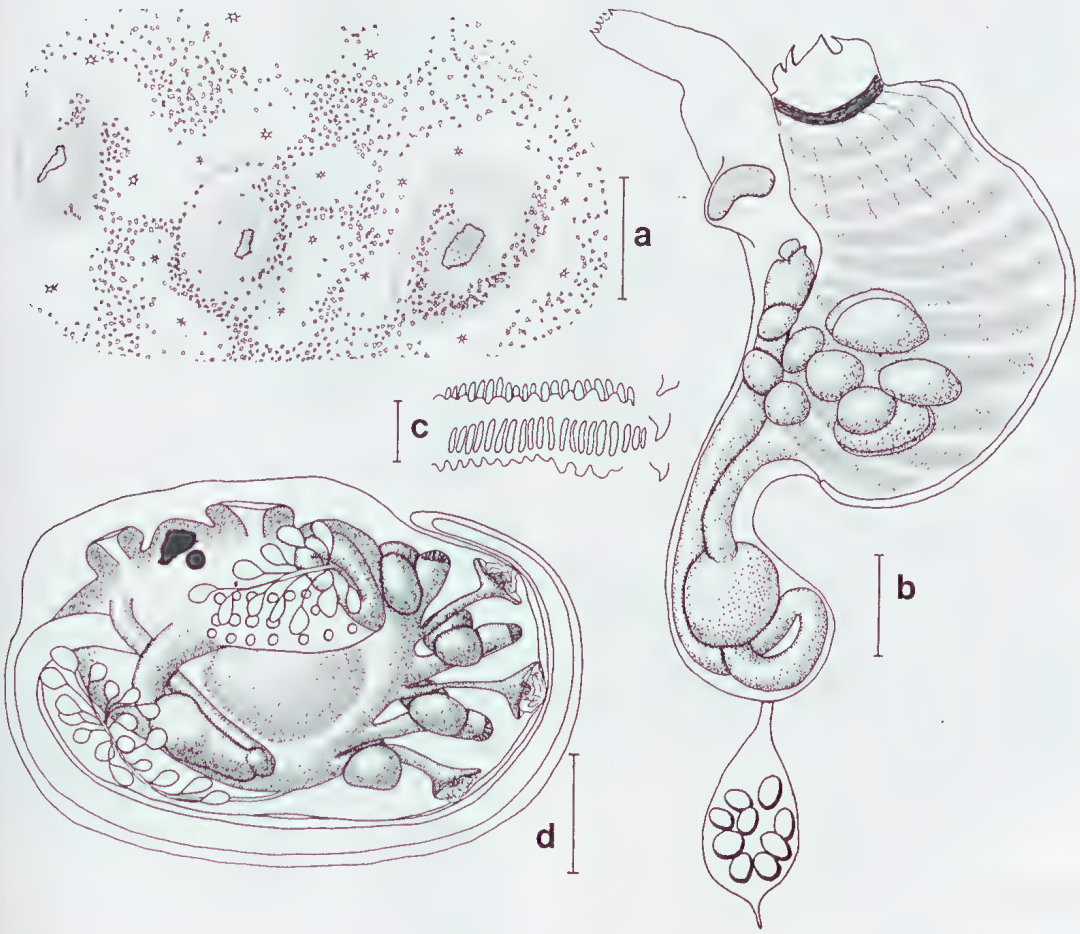


FIG. 30: *Polyclinum saturnium* — **a**, sandy surface of colony with large common cloacal apertures surrounded by branchial apertures (QM GH5034); **b**, zooid with 9 embryos in atrial cavity, abdomen twisted (QM GH5034); **c**, portion of branchial sac showing transverse vessels with papillae and dorsal languets (QM GH5035); **d**, larva (QM GH5035). Scales: **a**, 2mm; **b**, 0.5mm; **c**, 0.25mm; **d**, 0.1mm.

is moderately long and narrow with about 6 pointed denticulations on its terminal (straight) edge. Zooids have 8 to 12 rows of about 20 short, oval stigmata and about the same number of conspicuous, flat, tongue-shaped branchial papillae on the transverse vessels. These papillae are even more conspicuous anteriorly than posteriorly.

The gut forms the usual twisted loop. The bilabiate anus is halfway up the thorax. A group of about 8 large male follicles are clustered in a more or less spherical mass around the ova in the posterior end of the posterior abdomen.

About 5 embryos are scattered in the right peribranchial cavity of specimens collected from Bahiwasan (Philippines) in January (USNM 11540). Up to 10 embryos are present in the postero-dorsal quarter of the atrial cavity in specimens from Heron I. collected in May (QM GH5035). Tailed larvae have a trunk of 0.4 to 0.5mm, with the tail wound about three-quarters of the way around it. Median and lateral ectodermal ampullae have terminal caps of enlarged ectodermal cells. Paired rows of vesicles are antero-dorsal and postero-ventral.

REMARKS

The absence of the brood pouch distinguishes these specimens from *P. tsutsuii* (tropical) and *P. marsupiale* (temperate) which are also sandy, and have broad branchial sacs and circular or stellate systems. *Polyclinum incrustatum* and *P. solum* nom. nov. are also sandy species but they have narrower branchial sacs. The larvae have fewer ampullary vesicles than most other species of the genus.

The small specimen with only 8 rows of stigmata from Baliwasan assigned to *P. tsutsuii* by Tokioka (1967) seems more likely to be a specimen of the present species in which branchial sacs generally are shorter than in *P. tsutsuii*. The other small specimen (*P. vasculosum*: Tokioka, 1967 < *P. saturnium*) from Baliwasan has 10 to 12 rows of stigmata, as do the present colonies from Heron I. while *P. tsutsuii* has 14 to 16.

Polyclinum solum nom. nov.
(Fig. 31)

Polyclinum sabulosum Sluiter, 1909, p. 96

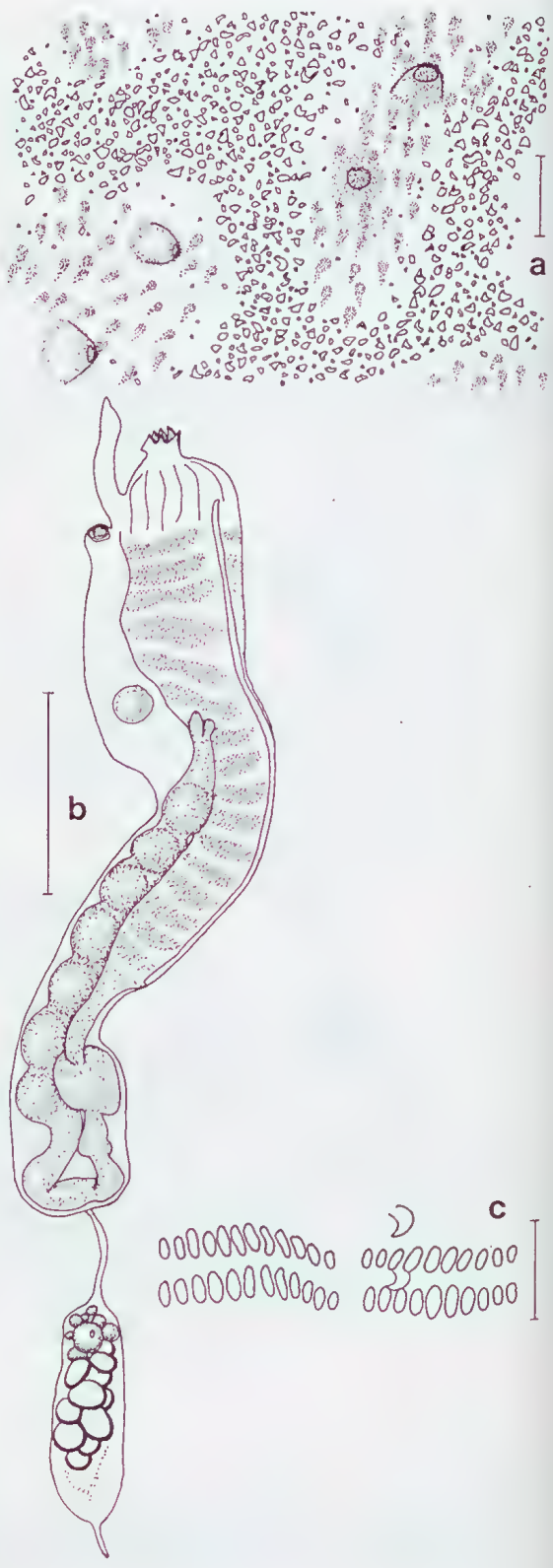


FIG. 31: *Polyclinum solum* nom. nov. — **a**, sandy surface of colony with protuberant common cloacal apertures surrounded by crowded branchial apertures (QM GH5023); **b**, zooid with single embryo in atrial cavity (QM G9293); **c**, portion of branchial sac (QM GH9293). Scales: **a**, 2mm; **b**, 1mm; **c**, 0.25mm.

DISTRIBUTION

NEW RECORDS: Queensland (Pt. Lookout, QM GH5273; Hervey Bay, QM G9293 G9295 GH4978–80; Tannum Sands S. of Gladstone, QM GH4977; Wistari Reef, QM GH5023; Heron I., QM GH5202 GH5273).

PREVIOUSLY RECORDED: Indonesia (Sluiter 1909).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are rounded cushions to 4cm in greatest extent and up to 1cm high. They have a single layer of sand grains adhering to the surface. Sometimes this is absent from the test over the systems, although it is present between and around them (QM GH5023). The internal test is very soft, transparent and free of sand. The cloacal apertures are on wart-like prominences about 3mm apart in the naked areas on the upper surface. Crowded zooids, some in short double rows, surround the cloacal apertures, and converge to them. Thoraces and abdomina are in the upper half of the colony and posterior abdomina in the lower half. There is no pigment in the test of the preserved specimens.

INTERNAL STRUCTURE: The zooids are slender, 6mm long, of which the thorax is about half. The abdomen is relatively short, but the loop is vertical rather than bending horizontally. The posterior abdomen is narrow and relatively long, more or less club-shaped, its posterior half slightly expanded. A fine vascular stolon extends from the tip of the posterior abdomen. Zooids contain minute dark pigment cells scattered through the body wall.

The 6 branchial lobes are triangular and pointed. A long, narrow atrial tongue extends from the body wall anterior to the muscular, forward-projecting atrial siphon. Six fine longitudinal muscles from the branchial siphon fade out on the anterior part of the thorax.

Fourteen to 18 rows of oval stigmata have 10 to 12 stigmata on the right and 12 to 14 on the left. There are some fine muscles in the branchial vessels, but there are no branchial papillae. The small smooth-walled stomach is halfway down the abdomen, with a moderately long duodenal area behind it. The vertical gut loop is twisted slightly so that the descending limb is ventral to the ascending limb, and the distal part of the loop is flexed slightly to the left. The rectum extends halfway up the thorax and the anal border is bilabiate.

Six to 10 male follicles are bunched or in an irregular double row in the posterior half of the long posterior abdomen, which is about twice the length of the abdomen. As they develop, they fill the whole of the posterior abdomen. The ovary is just anterior to them.

Colonies collected in November (QM GH4980) are in an active vegetative condition, those collected in May (QM GH4977) have mature male follicles.

REMARKS

Characteristics of the present species are the single layer of sand externally, the conical protuberant cloacal apertures, the narrow zooids with relatively few stigmata per row but numerous rows, the long narrow posterior abdomen with the gonads in its posterior half, testis follicles in an irregular double row, and the absence of branchial papillae. The holotype, from Indonesia, has a small tear-drop shaped posterior abdomen, like one of the juvenile colonies in the present collection (QM G9295). The Indonesian colony was stalked, and conical protruding cloacal apertures are not reported. However there is little else to separate the newly recorded specimens from it.

Polyclinum tenuatum n.sp. has similar (but smaller) crowded circular systems to the present species, but its zooids are smaller, branchial papillae are present, and the thorax is shorter. *Polyclinum constellatum*: Tokioka, 1967, has sand in the surface test, as does the present species. However, it has very numerous stigmata per row (15 to 20 and 40) and conspicuous branchial papillae. *Polyclinum saturnium* has similar colonies with prominent cloacal apertures and an external layer of sand. However it has a wide branchial sac with conspicuous papillae, relatively few rows of stigmata, and it lacks the narrow posterior abdomen of the present species.

Polyclinum solum nom. nov. replaces the name *P. sabulosum* Sluiter, 1909 for the present tropical species. The latter name is preoccupied by *Polyclinum sabulosum* (Lahille, 1890), which is a junior synonym of the northern hemisphere *Polyclinum aurantium* Milne Edwards, 1842.

Polyclinum tenuatum n.sp.
(Fig. 32. Plate 7a)

Synoicum papilliferum: Kott, 1963, p. 87.

DISTRIBUTION

TYPE LOCALITY: Western Australia (Shelly Beach, Nornalup, 29.1.39, holotype AM Y2261; paratypes AM Y1356).

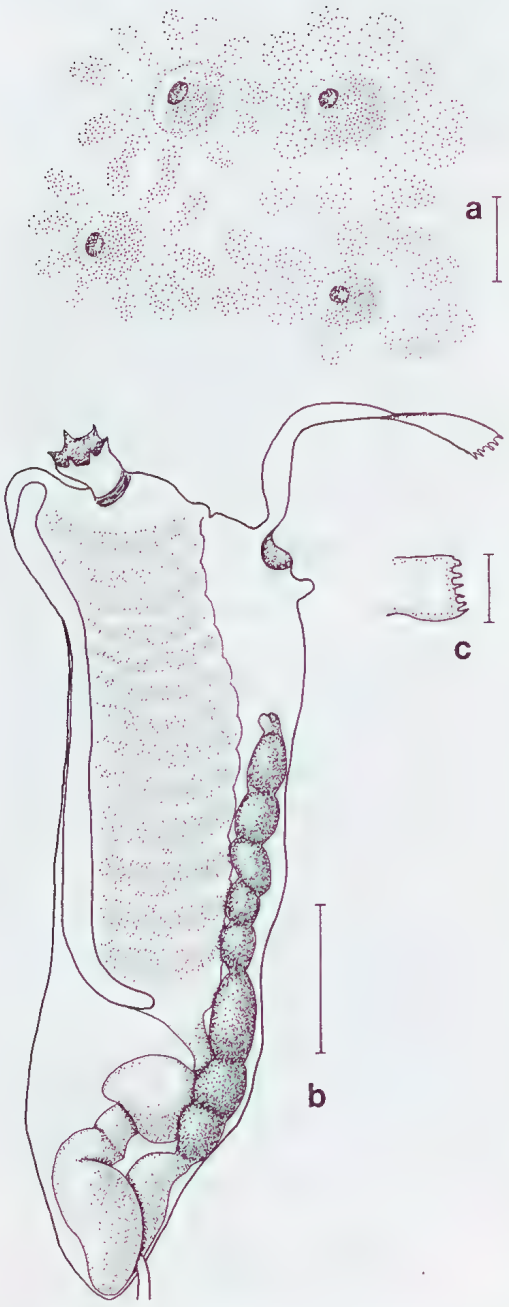


FIG. 32: *Polyclinum tenuatum* n.sp. — **a**, surface of colony showing zooids in circular systems with central common cloacal apertures (paratype AM Y1356); **b**, thorax and abdomen (QM GH5444); tip of atrial tongue (paratype AM Y1356). Scales: **a**, 1mm; **b**, 0.5mm; **c**, 0.1mm.

FURTHER RECORD: South Australia (Cape Jaffa, QM GH5444).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are fleshy sheets, up to 5mm thick, to 5cm in maximum extent, with an irregular outline, rounded borders, and a flat and even upper surface which has a light dusting of sand. The colonies are fixed to the substrate by irregular processes from the whole of the undersurface. Sand is sparse internally. Circular systems of 10 to 12 zooids have slightly protuberant common cloacal apertures in the centre of each system. Cloacal apertures are 2 to 3mm apart.

INTERNAL STRUCTURE: The thorax and abdomen are together about 3mm long. The posterior abdomen is short and sac-like or lengthened to a club-shape. Fine longitudinal muscles are confined to the anterior part of the zooid. The strap-like atrial tongue is produced forwards from the upper rim of the atrial siphon, which protrudes from the body wall. Five minute pointed papillae form a fringe along the straight tip of the atrial lip. A medial dorsal papilla projects from the body wall posterior to the base of the atrial siphon.

Thirteen rows of up to 12 relatively short, oval stigmata are separated by transverse vessels with about one conspicuous conical branchial papilla per stigma. The small, horizontal gut loop is twisted and the distal part of the loop curves forwards as is characteristic for the genus. The posterior abdomen, a short sac in its sexual phase, but long and club-shaped in the vegetative phase (QM GH5444), is attached by a narrow neck to the concavity of the distal curve of the gut loop.

REMARKS

Kott (1963), overlooking the branchial papillae and other characteristic polyclinid features (including the flexure of the gut loop and the constriction between abdomen and posterior abdomen), assigned these 3 colonies to *Synoicum papilliferum* on the basis of the dorsal papilla. This structure has since been found in many *Polyclinum* as well as *Synoicum* species.

The present species has a layer of sand on the upper surface, crowded circular systems, and the atrial lip from the upper rim of the aperture like *P. solum* from the central Queensland coast. However *P. solum* has a longer thorax with more rows of fewer stigmata, and lacks branchial papillae altogether. *Polyclinum terranum* n.sp. has similar branchial papillae and atrial lip, but its

zooids are larger, and its colonies have a keel-like structure anchoring them to the substrate.

Polyclinum terranum n.sp.
(Fig. 33. Plate 7b,c)

DISTRIBUTION
TYPE LOCALITY: Western Australia (Rockingham, 32°15.7S 115°37.1E, 15m, coll. AIMS Bioactivity Group 21.3.89, holotype QM GH5460).
FURTHER RECORDS: None.

DESCRIPTION
EXTERNAL APPEARANCE: The colony consists of extensive hard, robust zooid-bearing lamellae up to 1cm thick, 3cm across the upper surface and 6cm along its length, standing vertically above the substrate. Along the upper edge the thick zooid-bearing part curves over to form a round margin. Along the underside of the zooid bearing part, the colony abruptly changes to a keel-like flange (up to 0.5cm thick, 5cm deep) which is hard, brittle and stiff with embedded sand. This flange appears to have been embedded in sand, although here and there it suddenly increases in thickness to accommodate zooids, and it may have been above the surface of the substrate in those places.

The colony is complex, branched and folded so that lamellae lie in parallel against one other. Sometimes there are 2 basal keels attached to the one zooid-bearing part of the colony. Zooids are arranged in circular systems, about 3mm diameter, opening on the upper surface of the zooid-bearing part of the colony. Common cloacal apertures protrude from the surface. Patches of sand are present on the upper surface of the zooid-bearing part of the colony, and some is present internally, but it is sparse. The test is tough and zooids, tightly enclosed in it, are hard to remove. The atrial lip is inserted into the rim of the cloacal aperture and is particularly difficult to remove entire. In preservative the test is transparent, purple, but living specimens are a dark purple-brown, and opaque.

INTERNAL STRUCTURE: The thorax and abdomen together are about 4mm long, of which the abdomen is only about one quarter. Body wall musculature consists of about 6 fine longitudinal bands extending halfway down the thorax. Branchial apertures are small, with 6 pointed lobes. The atrial lip is long, moderately muscular with dorsal muscle bands extending along each side and transversely across the lip. The tip usually is pointed, terminating in 2 or 3 small papillae. The anterior part of the circular sphincter muscle of the atrial aperture is in the base of the atrial lip, and the lip is thus associated with the anterior rim of the aperture. A median dorsal papilla is behind the atrial aperture.

Sixteen rows of oval to rectangular stigmata with 15 in the middle rows are separated by transverse vessels containing the usual groups of transverse muscles. An extensive imperforate area of branchial wall is along each side of the endostyle. The transverse vessels have conspicuous, almost triangular branchial papillae, about one per stigma. The dorsal languets are small, only about twice the length of the branchial papillae.

The small gut loop has the usual twist distally, a smooth-walled stomach, long duodenum, and complicated course for the vas deferens. The bilabiate anus is halfway up the branchial sac. The posterior abdomen is tear-drop-shaped with a narrow neck attaching it to the abdomen. It contains mature gonads in the holoytpe colony, consisting of about 15 male follicles and 2 or 3 large eggs. Up to 2 embryos are in a brood pouch attached to the thorax by a narrow stalk, at the level of the anus.

Larvae have a trunk 0.7mm long with 2 median ampullae in each interspace between adjacent adhesive organs, 4 lateral epidermal ampullae on each side, and large postero-ventral and antero-dorsal clusters of epidermal vesicles on each side. Conspicuous caps of enlarged ectodermal cells are on the tips of the ampullae.

REMARKS
The present species, known only from its type locality off Rockhampton, resembles the southern Australian *P. incrustatum* and *P. tenuatum* in its circular systems. The latter species also has large branchial papillae and its atrial lip directly associated with the aperture.

Quite apart from the unique colony with its flat, brittle, keel-like extension projecting down into the substrate, *P. terranum* has more rows of stigmata and more stigmata per row than *P. tenuatum*. Although it has a similar number of stigmata to *P. incrustatum*, the latter species does not have a brood pouch. The brood pouch in the present species resembles that of *P. marsupiale* which, however, does not have the regular circular systems of the present species, and has fewer rows of stigmata and a slightly smaller (0.5mm trunk) larva.

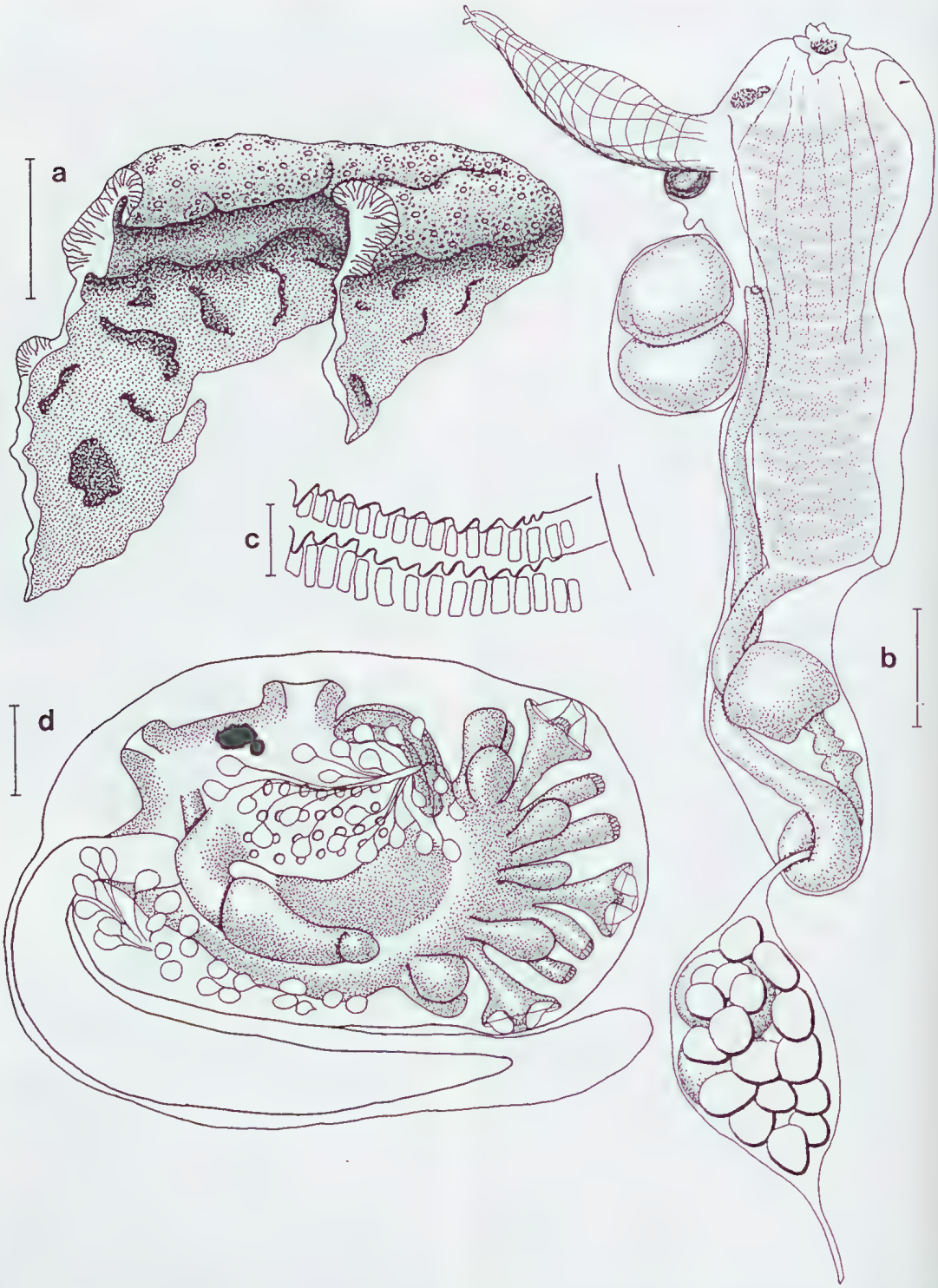


FIG. 33: *Polyclinum terranum* n.sp. (holotype QM GH5460) — **a**, portion of colony showing orientation of zooids in section at each end; **b**, zooid with 2 embryos in brood pouch; **c**, portion of branchial sac showing branchial papillae. **d**, larva. Scales: **a**, 2cm; **b**, 0.5mm; **c**, 0.2mm; **d**, 0.1mm.

Polyclinum tsutsuii Tokioka, 1954
(Fig. 34)

Polyclinum tsutsuii Tokioka, 1954a, p.240; 1967, p.47.
Polyclinum saturnium: Tokioka, 1962, p.260. Rho, 1966, p.212; 1971, p.108; 1975, p.126.
Polyclinum vasculosum: Tokioka, 1967, p.51 (part, specimen from Marianas Is).
Polyclinum pute: Monniot and Monniot, 1987, p.84. Monniot, 1987, p.514.
? *Polyclinum laxum* Van Name, 1945, p.71.

DISTRIBUTION
NEW RECORDS: Western Australia (W. of Cervantes, WAM475.91 476.91. Queensland (Heron I., QM GH5609).
PREVIOUSLY RECORDED: Moorea, Tahiti (Monniot and Monniot 1987). New Caledonia (Monniot 1987). Japan (Tokhara Is — Tokioka 1954a; Osaka, Sagami Bay — Tokioka 1962). Marianas Is (USNM 11540 Tokioka, 1967). Korea (Rho 1971, 1975). ? Eastern Pacific (Gulf of California — Van Name 1945).

The species has a wide longitudinal as well as latitudinal range in the Pacific Ocean.

DESCRIPTION
EXTERNAL APPEARANCE: Some colonies (WAM475.91) are sessile, rounded to wedge-shaped lobes, the borders sometimes spreading out in sheets over the substrate, other colonies are sheet-like and investing (USNM 11540). The external sandy coating often is light and interrupted on the upper surface leaving bare patches. Sand grains are sparse in the internal test. The zooids are in a crowded layer around the outside of the colony. The external layer of sand is interrupted where the zooids open to the surface, and the darkly pigmented anterior ends of the zooids are seen, evenly spaced over the surface. Zooids are difficult to remove from the test.

The actual arrangement of zooids is difficult to determine in some colonies, but in others they are seen to be arranged in crowded circular systems with the atrial lip inserted around the rim of the central common cloaca. However, it is possible that some cloacal canals with zooids along each side, radiate from the apertures.

INTERNAL STRUCTURE: Zooids are about 3mm long, including the short, tear-drop shaped posterior abdomen with a short neck attaching it to the abdomen. There is a posterior vascular stolon from the posterior end of the posterior abdomen.

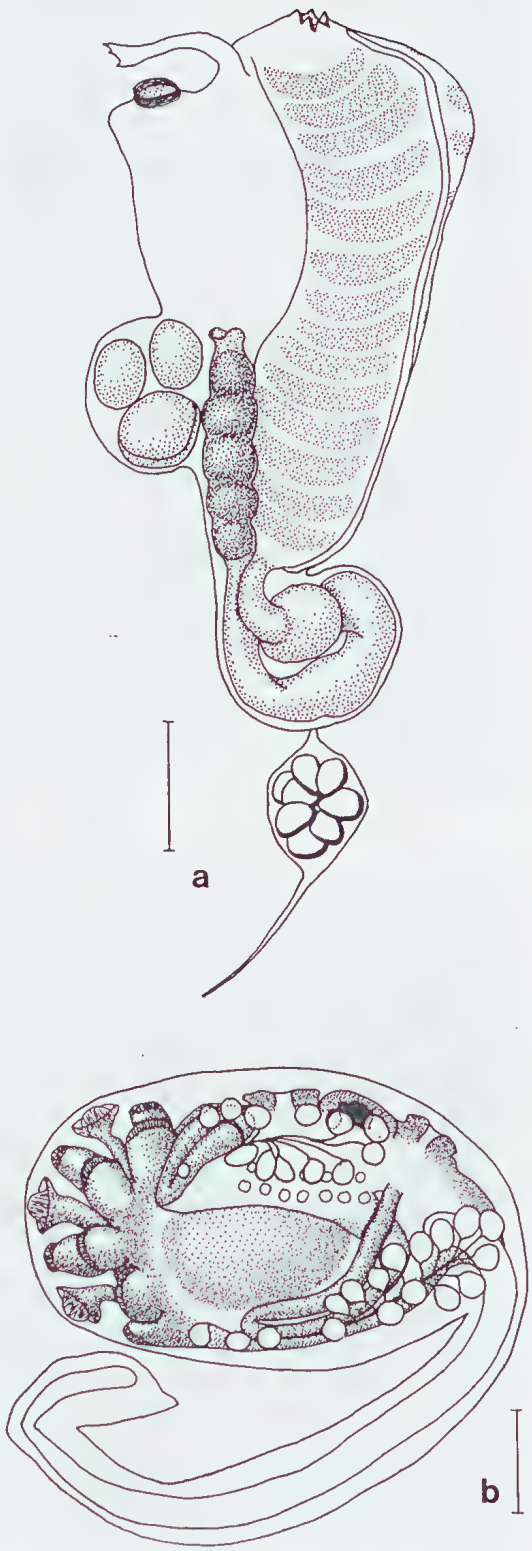


FIG. 34: *Polyclinum tsutsuii* — **a**, zooid with 3 embryos in atrial cavity (WAM 475.91); **b**, larva (WAM 476.91). Scales: **a**, 0.5mm; **b**, 0.1mm.

The atrial aperture is well anterior and the body wall projects dorsally so that the aperture is directed anteriorly. The atrial tongue is moderately long and fleshy, and sometimes has a serrated tip. Eight short, fine muscle bands on each side radiate from the branchial aperture over the anterior part of the body but they become finer posteriorly and only occasionally can be distinguished extending the whole length of the thorax. The branchial sac has 14 to 16 rows of about 18 to 20 stigmata per row. The transverse vessels have about one tongue-shaped papilla per stigma.

The gut loop is horizontal, lying close behind the thorax, with the distal part of the loop turned to the left. About 8 relatively large male follicles surround the ovary in the posterior abdomen.

Colonies taken in April have 3 embryos are in a brood pouch which projects from the dorsal part of the peribranchial cavity at about the level of the sixth row of stigmata. The larval trunk is 0.5mm long, with lateral and median ampullae alternating with the shallow, stalked, median adhesive organs. Ectodermal vesicles continue anteriorly in a row along each side of the median line from postero-ventral and antero-dorsal clumps. There is an otolith and ocellus. The tail is wound almost three quarters of the way around the trunk. The tips of the ampullae have caps of enlarged ectodermal cells.

REMARKS

The species is distinguished from *P. incrustatum*, which also has sand confined to the outer layer of test, by its wide branchial sac with 18 to 20 stigmata per row (instead of about 13), and its large larvae in a brood pouch rather than free in the atrial cavity. *Polyclinum incrustatum* has small, distinct circular systems with conspicuous projecting cloacal apertures which also distinguish it from the present species.

The sandy *P. solum* from the northeastern coast of Australia and Indonesia lacks branchial papillae; and has a long posterior abdomen with gonads in its posterior half, and a narrow branchial sac with only 8 to 10 stigmata per row.

Polyclinum saturnium, another sandy species is separated from the present one by the absence of a brood pouch, but has many other characters in common including a moderately long posterior abdominal neck and a broad branchial sac with about 20 stigmata per row. Specimens assigned to *P. saturnium* from Korea and Japan (see Tokioka 1962; Rho 1966, 1971, 1975) have the brood pouch characteristic of *P. tsutsuii*.

Polyclinum laxum Van Name, 1945, from the Gulf of California has potato-shaped colonies. Van Name thought this species could be a synonym of *P. saturnium* Savigny, 1816 (from the Gulf of Suez). However, embryos in *P. laxum* are probably in a brood pouch (see Van Name 1945) as they are in the present species but not in *P. saturnium*. The only difference evident between the Western Australian and the eastern Pacific specimens are that the latter have a longer oesophageal neck and the zooids do not seem to be so crowded.

Although Tokioka thought them to be unique, the short longitudinal thoracic muscles do occur in other species of this genus.

Polyclinum vasculosum Pizon, 1908
(Fig. 35)

Polyclinum vasculosum Pizon, 1908, p.223. Tokioka, 1967, p.51 (part, specimens from Hawaii).

Polyclinum macrophyllum Michaelsen, 1919, p.82; 1930, p.546 subsp. *phortax*. Hastings, 1931, p.105 subsp. *phortax*. Kott, 1963, p.82.

? *Polyclinum festum*: Van Name, 1918; p.162.

DISTRIBUTION

NEW RECORDS: Western Australia (Broome, WAM1023.83). New South Wales (Arrawarra, QM GH4986). Queensland (Pt Lookout, QM GH4981 GH4984; Myora, QM GH4985 GH4990 GH5027; Bribie I, QM G10124; Kawana Waters, QM GH4989; Noosa, QM GH1496; Pt Vernon, QM GH4991 GH4993 GH5028; Bargara, QM GH4983; Gladstone, QM GH4988; Capricorn Group, QM GH4992 GH4994–5018 GH5023–33 GH5185 GH5279; Lizard I., QM GH4982 GH5017 GH5025 GH5261–2 GH5268; off Cairns, QM GH4987).

PREVIOUSLY RECORDED: Western Australia (Shark Bay — Michaelsen 1930). Queensland (Capricorn Group — Kott 1963; Sarina, Mackay — Kott 1963; Low Is — Hastings 1931). ? Philippines (Van Name 1918). Indonesia (Pizon 1908). Hawaii (USNM 11755 Tokioka 1967). West Indian Ocean (Michaelsen 1919).

The species apparently is a tropical one.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are naked, fleshy, extensive investing sheets or cushions to about 2cm thick. In life thinner sheets are brown, yellowish brown and beige internally. Thicker specimens are greenish-black, to black, often with some yellow, and 'mummy brown' (Ridgeway 1886) internally. In preservative they are brown, red-brown to pink. The test is firm and gelatinous, and does not have embedded sand.

Zooids are arranged in rows along each side of branching canals that radiate from the cloacal apertures. In relatively thin colonies with thin surface test the cloacal apertures are completely sessile, sometimes opening out along the top of the parts of the cloacal canals adjacent to them. They have denticulate borders which contain the tips of the long atrial lips of the zooids in their vicinity. Zooids further away have their atrial lips stretched out with their tips inserted into the test above the canals. The atrial lips contain brown pigment making them very conspicuous through the surface test, outlining not only the cloacal apertures, but also the branching canals, which, when they are crowded, often appear to form a network.

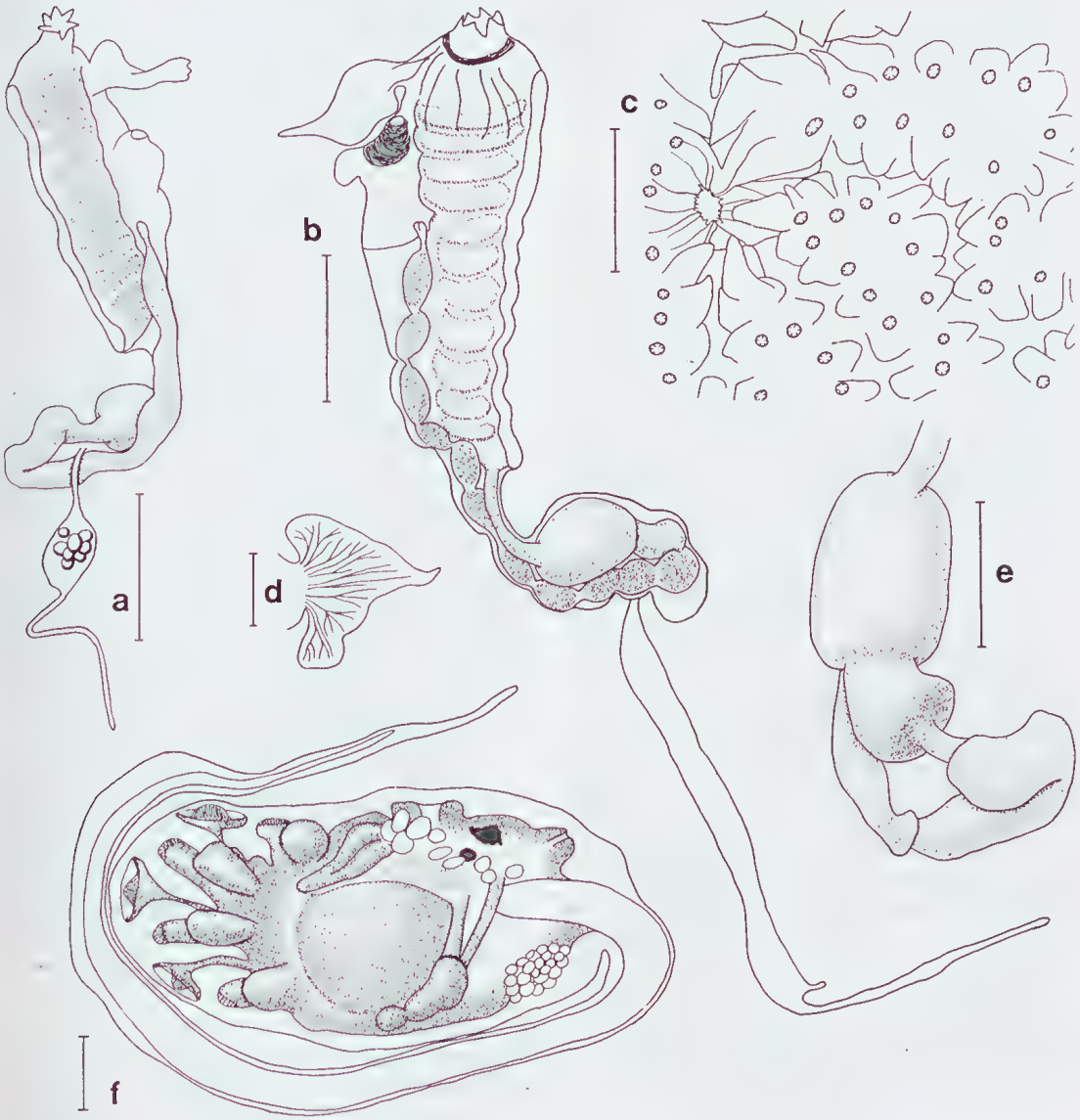


FIG. 35: *Polyclinum vasculosum* — **a**, **b**, zooids (**a**, QM GH1496 with sexual posterior abdomen; **b**, QM GH4984 with vegetative posterior abdomen); **c**, colony showing atrial lips along each side of cloacal canals that converge to common cloacal apertures (QM GH4982); **d**, atrial lip (QM GH4984); **e**, gut loop (QM GH4984); **f**, larva (QM GH4985). Scales: **a**, **b**, 1mm; **c**, 2mm; **d**, **e**, 0.5mm; **f**, 0.1mm.

Thicker colonies, which are recorded from mainland rather than coralline habitats, have less conspicuous systems, and cloacal and zooid apertures. The thick surface test obscures the openings, the denticulations around them, the insertion of the tips of the atrial apertures into the test and the position of the zooids relative to cloacal canals. Sometimes common cloacal apertures are raised on slight conical prominences about 1cm apart and are evenly distributed over the surface. In other specimens each branchial and cloacal aperture is depressed into the surface. In some colonies zooid-free areas of test separate the systems, which have cloacal apertures about 5mm apart. In others, the cloacal systems are contiguous and the only zooid-free parts of the test are those between the rows of zooids.

Vesicles (about 0.04mm in diameter) are evenly scattered in the surface test, about 0.3mm apart, amongst zooid openings, although they often are obscured by zooids and pigment.

INTERNAL STRUCTURE: Zooids in the thinner colonies are more easily removed from the test than those in the thicker ones, which have the atrial lips embedded in thicker, firmer test. The thorax is large and roomy (up to 3mm long). Usually the smaller abdomen (about 2mm long) is bent at right angles to the thorax. The posterior abdomen varies from the short, sac-like sexual organ to the long (up to 3mm) strap-like vegetative one. A delicate, sometimes branched, vascular stolon extends into the test from the end of the posterior abdomen.

The branchial lobes are well-formed and triangular. The atrial lip is long and broad, and usually constricted at the base. Its shape is variable, being tongue-shaped or short and broad with up to 7 denticulations on its outer edge, or leaf-shaped, tapering to a single point. It contains longitudinal muscle bands that extend into it from the dorsal side of the branchial siphon. These divide into separate fibres toward the sides and tip of the lip. The atrial aperture surrounded with circular muscles protrudes forwards on a short siphon, beneath the atrial lip. There is a median dorsal papilla protruding from the body wall posterior to the atrial siphon. About 10 to 15 fine longitudinal thoracic muscles extend from the branchial siphon to about one third of way down the thorax. There are 12 to 14 rows of short oval to rectangular stigmata, the latter being in larger, mature zooids. The dorsal languets are to the left of the mid line, and there are 2 more stigmata on the left than on the right side of the zooid. Stigmata vary from 8 on the right side posteriorly to 16 on the left side anteriorly.

In some colonies (possibly with juvenile zooids) the stigmata are small and oval and rounded papillae are on the transverse vessels (Gladstone QM GH4988). However, this is rare, and papillae were not usually detected.

The oesophagus is relatively long and distally it bends before entering the smooth, oval horizontal stomach, which lies anterior to a horizontal part of the rectum in the ascending limb of the gut loop. The distal end of the loop curves to the left and dorsally and the short neck connecting it to the posterior abdomen is on its dorsal side. The rectum extends anteriorly to halfway up the branchial sac and ends in a 2-lipped anus.

The sexual posterior abdomina are short, teardrop-shaped containing male follicles and ovary. These lengthen to comma shaped organs and subsequently to long and strap-like vegetative posterior abdomina. The latter are found on vegetative zooids around the actively growing borders of the colony. Comma-shaped posterior abdomina with the V-shaped heart posteriorly and a few male follicles and small ovary in the middle or anteriorly, occur as the zooid changes from its sexual to vegetative phase.

Two or 3 embryos are found in the unusually large atrial cavity of zooids collected in May in Moreton Bay, August (but not in March) from the Capricorn Group and in June from Lizard I. The embryos are few and small, especially in relation to the thorax and its roomy peribranchial cavity. It is possible that the species compensates for this by a long reproductive period (producing offspring over much of the year), and by having large long-lived colonies with numerous zooids.

The larval trunks are 0.5 to 0.6mm long. They have 3 shallow, narrow-stalked adhesive organs anteriorly, alternating with median and lateral ampulla, and a postero-ventral and mid-dorsal clump of ectodermal vesicles. The ampullae have conspicuous caps of enlarged epidermal cells, and similar enlarged ectodermal cells are present in the outer walls of the ectodermal vesicles.

REMARKS

Polyclinum vasculosum Pizon, 1908 from Indonesia was described from a small, single system colony. The zooids in branching double rows radiate from the common cloaca. The zooids have 12 rows of stigmata with up to 15 stigmata per row, and no branchial papillae were detected on the transverse vessels. Specimens from Hawaii, the Philippine and Marianas Is., some sandy and

others naked, were assigned to this species (Tokioka 1967), but the naked ones (from the Hawaiian Islands) are the only ones correctly assigned. They have branching double rows of zooids radiating from large cloacal apertures with denticulate borders (like those of *P. constellatum*: see colonies from St. Helena, Michaelsen 1930), dark pigment (yellowish-brown) in the zooids, and colonies that are extensive sheets up to 2.5cm thick. The narrow thoraces, dark pigment, long atrial languets and large cloacal apertures resemble *Polyclinum macrophyllum* which appears to be a synonym of *P. vasculosum*. *Polyclinum festum* Van Name, 1918 from the Philippines, which has large investing colonies, is probably also a synonym of *P. vasculosum*, although the colonies are too mutilated to be sure.

Polyclinum macrophyllum Michaelsen, 1919 from Malagasy, and Western Australia (Michaelsen 1930), with its large muscular atrial lip, narrow thorax, 12 to 14 rows of 10 or 11 stigmata and branchial papillae sometimes on the transverse vessels, cannot be separated from *P. vasculosum*, especially from colonies from the Hawaiian islands (Tokioka 1967). Michaelsen distinguished *Polyclinum macrophyllum phortax* Michaelsen 1930 (from Shark Bay, Western Australia) from the West Indian Ocean *P. macrophyllum typicum* by its almost rough (rather than smooth and slippery) upper surface, the tighter insertion of the atrial tongue into the surface layer of test, and more delicate atrial musculature. However, these distinctions fall within the range of variation of the Australian populations and there well may be a continuous distribution around the Indian Ocean. Thus, assuming the synonymy of *P. macrophyllum* with *P. vasculosum* Pizon, 1908 is valid, *P. vasculosum* has a range from the West Indian Ocean into the Western Pacific to Hawaii (see Tokioka, 1967).

Polyclinum festum Hartmeyer, 1905 from Mauritius has a long, narrow atrial lip and probably does not belong to this species. Although its surface is smooth, sand is present on the base and sides of the colony and sometimes on the surface (see Millar 1975).

The large (6mm) investing colonies, *Polyclinum festum*: Van Name, 1918, from the Philippines, although so mutilated that systems could not be discerned, probably are synonyms of the present species. Van Name (1945) believed that these specimens, as well as *P. festum* from the type locality to be synonyms of *P. constellatum* which also has its type locality in Mauritius. However, all 3 species appear to be distinct. Michaelsen (1930) believed that *P. constellatum* could be distinguished by its branching double row systems while in *P. macrophyllum* (< *P. vasculosum*) branching canals formed a network. However, the complicated branching cloacal canals with a row of zooids along each side, that converge to the cloacal apertures, occur in both species. The primary difference between them appears to be the shape of the colony, viz. a capitate cushion attached by a small area of the base in *P. constellatum*, and in the present species an extensive sheet fixed by the whole of the basal surface. Usually the absence of branchial papillae also is indicative of *P. vasculosum*.

Genus **Aplidiopsis** Lahille, 1890

Type species: *Macroclinum vitreum* Lahille, 1887

Species of this genus resemble those of *Polyclinum*. The zooids differ mainly in the absence of branchial papillae, the relatively large and vertical gut loop, and in some species a ventral band of muscles continuing onto the abdomen and posterior abdomen. As in *Polyclinum* the posterior abdomen is connected to the abdomen by a narrow neck, and the vas deferens takes the characteristic polyclinid course from the left to the right side of the gut loop. As in *Polyclinum*, *Synoicum* and *Sidneioides* the oesophagus curves ventrally to enter the stomach along its dorsal border. A long atrial lip sometimes extends out from the upper rim of the opening as in *Synoicum* spp. and some *Polyclinum* spp. (e.g. *P. orbitum*). In other species the atrial lip arises from the body wall anterior to the opening and closes down over the anteriorly oriented atrial aperture, as in most *Polyclinum* spp. and some *Synoicum* spp. Zooids are arranged in circular or stellate systems.

Generally *Aplidiopsis* zooids are about 1cm long while those of *Polyclinum* are about 5mm or less. Other differences between *Polyclinum* and *Aplidiopsis* are discussed above (see Polyclinidae). The relatively large, vertical gut loop and the larger zooids of *Aplidiopsis* are very often the only reliable characters to distinguish it from *Polyclinum*. Although the posterior abdomen and testis are longer than in *Polyclinum*, the gut loop is vertical rather than horizontal, and the characteristic twist found in *Polyclinum* does not occur in this genus, a relationship to *Polyclinum* is indicated by the ocurse of the vas deferens.

Aplidiopsis is not diverse. In addition to the type species from the Mediterranean, the known

species are *A. pannosa* (Ritter) from Alaska (see Nishikawa 1990) and the related *A. helenae* Redikorzev (see Van Name 1945), *A. atlantica* Monniot, 1974 from the Azores (at 600m), *A. stellata* Monniot and Monniot, 1984 from Guadaloupe, *A. pyriformis* (Herdman, 1886), *A. amoyense* Tokioka, 1967 from China, *A. tokaraensis* Tokioka, 1954a from the Tokhara Is, *A. discoveryi* Millar, 1960 from the North I. (New Zealand), and 3 new Australian species (see below). *Aplidiopsis pannosa*, *A. atlantica*, *A. stellata* and *A. helenae*, *A. confluata* n.sp., and *A. mammillata* n.sp., have delicate muscles confined to the anterior part of the thorax, in contrast to the other known species, which have the thoracic longitudinal muscles converging to a ventral band that extends the length of the zooid. *Aplidiopsis stellata* is known to have a brood pouch at the posterior end of the thorax rather than halfway up as in *Polyclinum*. The 3 species recorded from Australia are from temperate waters.

Key to species of *Aplidiopsis* recorded from Australia

1. Longitudinal muscles extend the length of the zooid; systems circular ..... *A. sabulosa* n.sp.

   Longitudinal muscles do not extend the length of the zooid; systems not circular 2

2. Colony sandy; common cloacal apertures protrude ..... *A. mammillata* n.sp.

   Colony not sandy; common cloacal apertures sessile ..... *A. confluata* n.sp.

Species recorded from waters adjacent to Australia

Aplidiopsis amoyense Tokioka, 1967 from Hsia-men has stellate systems that resemble those of *A. mammillata* n.sp. (see below).

Aplidiopsis discoveryi Millar, 1960 from New Zealand, unlike *A. sabulosa* n.sp., lacks sand altogether. The zooids, arranged in circular systems, can be seen through the transparent test.

Aplidiopsis tokaraensis Tokioka, 1954a from the Tokhara Is have an external layer of sand obscuring the systems. About 10 longitudinal thoracic muscles converge to form a ventral abdominal band. Monniot (1974) believed this species to be a member of the genus *Sidnyum*, with 8 branchial lobes. However, its smooth stomach wall shape of the posterior abdomen preclude that view.

Aplidiopsis confluata n.sp.
(Fig. 36)

DISTRIBUTION

TYPE LOCALITY: Tasmania (Ninepin Point, 5m coll. P. Last 19.7.82, holotype QM GH5514).

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: The colony is a soft, almost spherical, naked head, about 2.5cm in diameter, attached by a short, thick, wrinkled stalk which narrows toward the base, and has some sand adhering to it. Double rows of zooids converge to large, sessile common cloacal apertures which are scattered randomly over the head. The test is soft and translucent internally, though the surface layer is opaque. Zooids are crowded, and cross one another in the centre of the colony and down into the stalk. The test, although it is soft, is tough and the zooids, tightly enclosed in it, are difficult to free from the colony.

INTERNAL STRUCTURE: Zooids are at least 1cm long, of which the thorax is about 2mm the abdomen about 1mm, the posterior abdomen occupying most of the zooid length. The branchial aperture has 6 small, pointed lobes. There is a long, flat, strap-like tongue from the body near the anterior edge of the first row of stigmata. The atrial aperture, with a sphincter muscle, is opposite the second row. About 8 fine longitudinal muscles on each side radiate from the branchial aperture and fade out halfway down the thorax. A median dorsal papilla is posterior to the atrial aperture. There are 16 rows of up to 14 stigmata, the ventral ones progressively reduced in length. The gut loop is vertical, although the oesophagus curves ventrally to enter the smooth-walled stomach. The duodenum expands in diameter to its junction with the short proximal part of the midintestine, and an oval posterior stomach is in the descending limb of the gut loop.

The posterior abdomen is particularly long, extending into the centre of the colony and down into the stalk. It is joined to the left (or ventral) side of the pole of the gut loop by a short narrow neck, but distal to the neck it abruptly increases in diameter and the greater part of the posterior abdomen is of even diameter. Anteriorly gonads are absent from 5mm or more of its length. They occupy about 2mm of the middle part of the posterior abdomen. They consist of a small ovary anteriorly, and a long cluster of almost spherical testis follicles. These are of various sizes, randomly distributed in the cluster, and they are not

in regular longitudinal series. The vas deferens curves around the gut loop onto the other (right or dorsal) side to extend anteriorly to the atrial cavity between the oesophagus and rectum. There are no embryos in this specimen.

REMARKS

The species is unique in its soft sand-free test, crowded zooids and their long posterior abdomina each with a long bunch of testis follicles about half way down. It resembles the other Australian species *Aplidiopsis mammillata* n.sp. in its long longitudinal muscles confined to the anterior part of the long, delicate thorax, and the absence of branchial papillae. The long, strap-like atrial tongue is more conspicuous, there are more stigmata per row but fewer rows, and the posterior abdomen is longer than in either of the other 2 Australian species assigned to this genus. *Aplidiopsis discoveryi* Millar, 1960, from New Zealand has circular systems and a spindle-shaped posterior abdomen distinguishing it from the present species.

Aplidiopsis mammillata n.sp.
(Fig. 37. Plate 7d)

DISTRIBUTION

TYPE LOCALITY: South Australia (Cathedral Rock, near Thistle I., Spencer Gulf, coll. W.H. Sasse 6.4.87, slide 19, holotype QM GH4168).

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: The holotype is a large cushion 4cm in diameter and 1cm thick. The upper surface is depressed and divided into 3 naked areas by raised sandy elevations continuous with the raised rim around the margin. There are one or 2 systems in each naked area. Each system has sandy strips extending along radii from the peripheral sandy elevated rim to the central protuberant common cloacal aperture. Three or 4 double rows of zooids extend out between the radial strips of sand. Sand is confined to the surface test, however, and never is found internally. Zooids are tightly enclosed in the soft test and are difficult to remove.

INTERNAL STRUCTURE: The zooids are large, 7mm long, the thorax being more than half of the total length. The branchial aperture is small with

FIG. 36: *Aplidiopsis confluata* n.sp. (holotype QM GH5514) — a, colony; b, zooid. Scales: a, 2cm; b, 0.5mm.

6 pointed lobes. The small anteriorly directed atrial aperture is near the anterior end of the zooid.

Fine and inconspicuous longitudinal muscles were detected in the anterior part of each zooid. The atrial lip is long and narrow, arising from the body wall, and is difficult to remove from the test. There are 18 rows of stigmata with about 10 per row. The gut loop is vertical and relatively short. The stomach wall is smooth.

A long, almost cylindrical posterior abdomen, with a narrow neck attaching it to the left side of the gut loop, contains crowded male follicles and a small ovary surrounded by the male follicles.

REMARKS

Aplidiopsis amoyense Tokioka, 1967 from Hsia-men has stellate systems that resemble those of this new South Australian species. Zooids are also similar, with only very delicate muscles, however the Australian species has a larger branchial sac with about 18 rows of stigmata (the Chinese species having 12), and sand adheres to the external test.

Aplidiopsis pannosa is also in this group of species, with delicate muscles, and a smaller gut loop than usual. However, it lacks the characteristic radiating double row systems of *A. amoyense* and the present species.

Aplidiopsis sabulosa n.sp.
(Fig. 38. Plate 7e)

DISTRIBUTION

TYPE LOCALITY: South Australia (Price I., Avoid Bay 15–20m, coll. W.H. Sasse 9.4.87, holotype QM GH4153).

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: The holotype is a large cushion 10cm in diameter up to 3cm thick and with sand embedded throughout, absent only from the surface around the branchial and common cloacal apertures. The surface is even, without depressions or ridges. The cushion is fixed by a small area of the flat basal surface. Zooids open onto the rounded borders of the colony as well as its upper surface and much of the basal surface as well. Zooids are arranged in circular systems around sessile conspicuously naked common cloacal apertures about 5mm apart.

INTERNAL STRUCTURE: Zooids are about 1.3cm long of which the thorax and abdomen are of equal length and together are about half the total zooid length. Six strong longitudinal muscles from the branchial aperture, with some from the intersiphonal space, extend to the posterior end of the thorax where they join into a single ventral band that extends to the end of the zooid. The atrial lip is a tongue-shaped muscular extension of the upper border of the opening. It is forked at the tip. The atrial opening is anteriorly directed.

There are 20 rows of about 6 stigmata. The gut loop is voluminous. The oesophagus curves into the stomach which has a short dorsal border and a long, curved ventral margin. The duodenum is long and there is an oval posterior stomach at the bottom of the descending limb of the loop. The rectum extends to about halfway up the thorax,

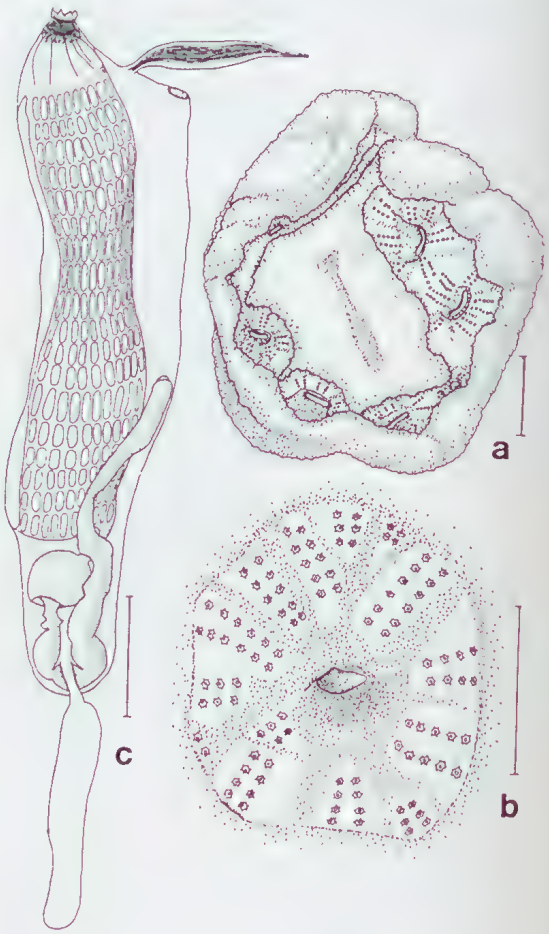
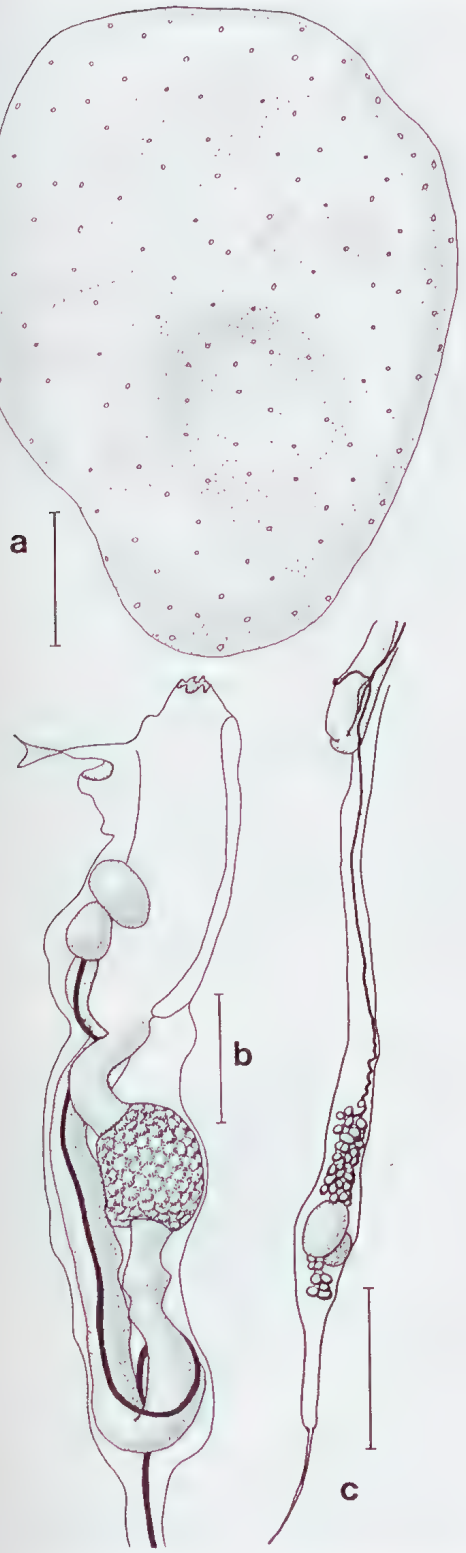


FIG. 37: *Aplidiopsis mammillata* n.sp. (holotype QM GH4168) — **a**, colony from above; **b**, single system with central protuberant cloacal aperture and double rows of zooids converging to it; **c**, zooid. Scales: **a**, 1cm; **b**, 5mm; **c**, 1mm.



terminating in a bilabiate anus. The stomach wall has internal circular patches of glandular epithelium giving a mulberry-like pattern.

The posterior abdomen is long, with a narrow neck anteriorly joining it to the left side of the pole of the gut loop. This neck portion gradually expands to the posterior gonad-bearing half. Male follicles are small and bunched and the large 2-egg ovary is surrounded by them. At its posterior end, the posterior abdomen tapers to a vascular stolon. The vas deferens curves around the ventral side of the posterior stomach from the left (or ventral) side of the loop and extends along the right side of the curve and inner side of the rectum to open at the level of the anus.

Two or 3 early embryos crowded in a longitudinal series are in the posterior part of the atrial cavity of the holotype (collected in April). Tailed larvae were not present.

REMARKS

Aplidiopsis mammillata has about the same number of rows of stigmata as the present species, but slightly more per row. It is also distinguished by its delicate musculature, smaller gut loop, smooth stomach wall, short and cylindrical posterior abdomen and its radial double-row systems.

Aplidiopsis sabulosa has circular systems like *A. discoveryi*, and *A. confluata*, and is distinguished by its embedded sand, and small number of stigmata in each row.

Aplidiopsis tokaraensis has sand on the outer surface, but not embedded in the test. The zooids have 18-20 stigmata and 12 rows, clearly distinguishing them from zooids of the present species.

Genus **Sidneioides** Kesteven, 1909

Type species: *Sidneioides tamaramae* Kesteven, 1909.

The genus resembles *Polyclinum* in its short longitudinal muscles, large muscular atrial lip that arises from the body wall anterior to the opening and its smooth-walled and bilaterally symmetrical stomach. It differs in having a relatively large ovary. The position of the ovary at mid-thoracic level, and a relatively large vertical gut loop. A median dorsal papilla projects from

FIG. 38: *Aplidiopsis sabulosa* n.sp. (holotype QM GH4153) — **a**, colony from above; **b**, thorax and abdomen with 2 embryos in atrial cavity; **c**, posterior abdomen. Scales: **a**, 2cm; **b**, 1mm; **c**, 2mm.

the body wall behind the atrial aperture as in many species of *Polyclinum* and *Synoicum*. The vas deferens passes around the ventral side of the descending gut loop to lie on the right side of the rectum as in *Polyclinum*. The voluminous vertical gut loop, absence of branchial papillae, and long posterior abdomen are more like *Aplidiopsis* than *Polyclinum*.

The larvae are small, sometimes smaller than those of *Polyclinum*. Although they have similar lateral ampullae and ectodermal vesicles, median ampullae are not present.

Three species of this genus are known. One is indigenous, with a wide range (from Westernport to Gladstone) on the eastern coast of Australia. The other known species are recorded from Japan (see Tokioka 1953):

Sidneioides japonense Redikorzev, 1913, recorded from Japan and Indonesia (Tokioka 1953, Millar 1975, Nishikawa 1990) forms a flat cushion with irregular furrows and protruding cloacal apertures on the upper surface. As in *S. tamaramae* a layer of sand adheres to the surface test, but sand is not present internally. The species are distinguished by their colony shape, and by the longer rows of stigmata and longer larval trunk of *S. japonense* (see Tokioka 1953).

Sidneioides snamoti (Oka, 1927) is distinguished by its systems which resemble those of *Polyclinum vasculosum*, with branching cloacal canals converging to protuberant cloacal apertures. The zooids differ from those of other species in having more rows of stigmata (17 to 19), as well as a large number of perforations in each row (see also Tokioka 1953, Nishikawa 1990).

Sidneioides tamaramae Kesteven, 1909
(Fig. 39. Plate 7f)

Sidneioides tamaramae Kesteven, 1909, p.277, Kott, 1957, p.104; 1976, p.63.

DISTRIBUTION

NEW RECORDS: New South Wales (Ulladulla, QM G11859; Twofold Bay, AM Y2151; Merewether, MV). Queensland (Gladstone Harbour, QM G9808).

PREVIOUSLY RECORDED: Victoria (Western Port — Kott 1976). New South Wales (Tamaramae Bay — Kesteven 1909; Merewether — AM Y1318–9 U3831 Kott 1957).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies consist of upright mushroom-shaped lobes widest across their free ends where often they are subdivided into separate shallow lobes, each with a central protruding cloacal aperture. Branchial openings are inside a ridge around the outer margin of each subdivision. The colony lobes narrow toward the base where they are continuous with the basal common test. The small colonies from Gladstone are separate lobes, without the basal common test (QM G9808). The diameter across the free end of each terminal branch is about 1cm, and the rounded subdivisions each containing a single circular system, are about 0.3mm in diameter. The free terminal part of each lobe is nearly 1cm long, and the overall height of the colony is up to 3cm. The whole outer surface is covered with a thick layer of sand. Sand is not present internally. Although the test is rather tough, the whole colony is soft, flaccid, and colourless in preservative. The outer free ends of all the lobes are level with one another and crowded together, and the upper surface has a cauliflower-like appearance. The large, muscular atrial lip of each zooid is extended into the central of the colony lobe and is inserted into the test around the cloacal aperture.

INTERNAL STRUCTURE: The zooids are about 6mm long including the posterior abdomen, which is attached to the abdomen by a long, narrow neck. The thorax is about two-thirds of the length of the abdomen. Six to 10 fine longitudinal muscle bands are on the anterior half of the thorax. The atrial aperture is projected forwards, and the anterior atrial lip, containing longitudinal and fine transverse muscles arises from the body wall anterior to the aperture. Twelve to 14 rows of stigmata, each with about 12 stigmata, are separated from one another by plain-edged transverse vessels each containing a narrow band of muscles.

The voluminous gut loop is vertical and the stomach smooth-walled. The posterior abdomen, joined to the abdomen by a narrow neck, is short, tear-drop-shaped to long and almost cylindrical or elliptical and is packed with male follicles. The relatively large ovary, with up to 18 eggs of various sizes, is in the thorax just on the right side of the anal opening, half way up the thorax. The colony from Gladstone collected in April has up to 8 embryos in the anterior half of the right peribranchial cavity.

The larval trunk is 0.4mm long (one of the smaller viviparous larvae known in the Ascidiacea). The tail is wound almost the whole way around it. Four lateral ampullae are present each side of the adhesive organs, and there are clumps of postero-ventral ectodermal vesicles each side of the base of the tail, and a row of about 6

ectodermal vesicles along each side of the mid-dorsal line.

REMARKS

The colony closely resembles that of *Polyclinum orbitum*. The shape and consistency of the colonial lobes are the same, and both zooids and larvae are very similar in size in these two species. The larvae of the present species, also resemble those of *P. orbitum* in the absence of median ampullae. *Sidneioides tamaramae* can be distinguished by the absence of branchial papillae, the position of the ovary, and the atrial lip, which in *P. orbitum* extends out from the upper rim of the aperture (as it does in *Aplidiopsis*, but seldom in other species of *Polyclinum*). The present species also has fewer rows of stigmata, fewer stigmata per row, and a larger and more vertical gut loop than *P. orbitum*.

The thickness of the basal common test varies, the type specimens having a basal plate (Kesteven 1909) rather than the upright stalk of the newly recorded colonies from Ulladulla (QM G11859).

Genus **Synoicum** Phipps, 1774

Type species: *Synoicum turgens* Phipps, 1774.

Zooids are small, and form circular or double-row systems. Colonies are sessile cushions, or investing sheets, or stalked heads. Despite the small size of the zooids there are 4 to 20 rows of

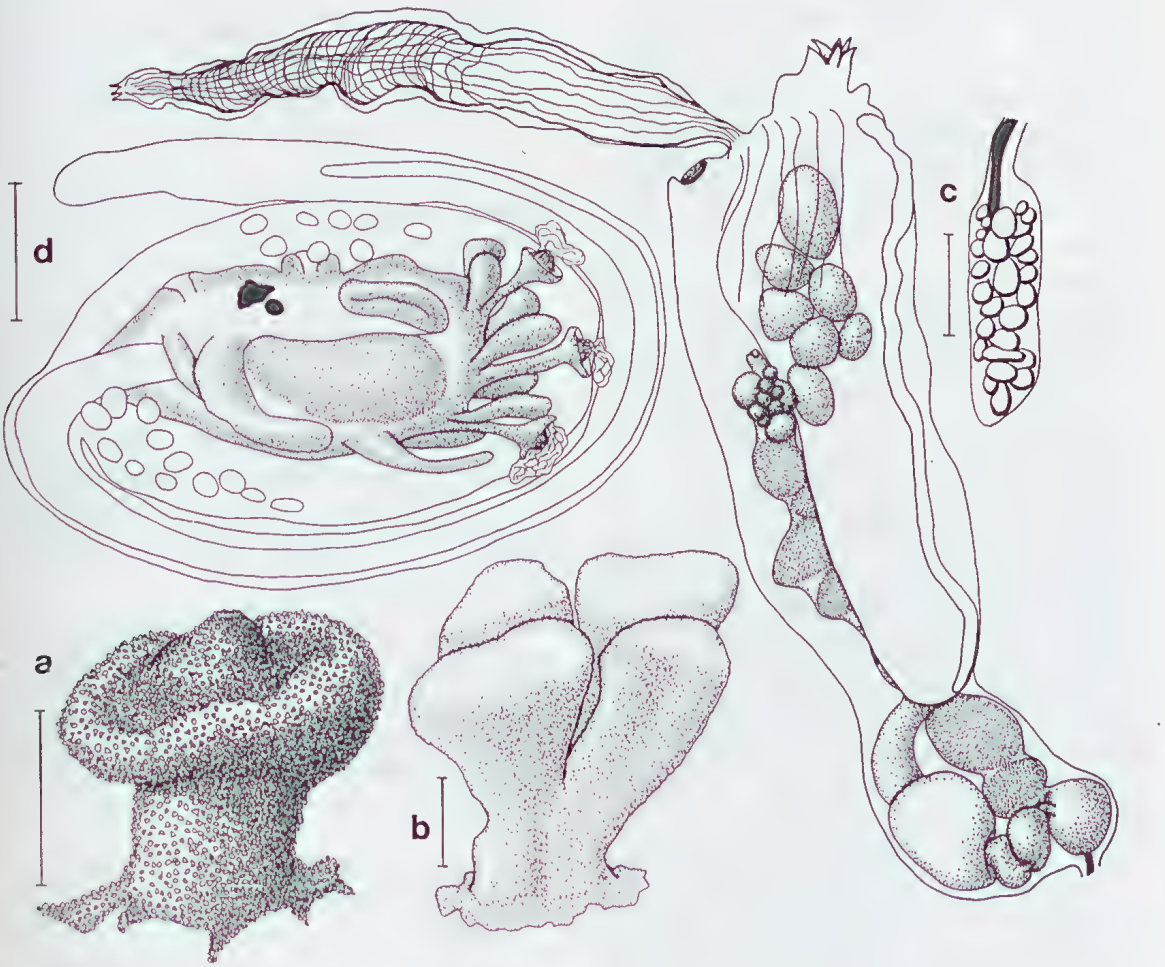


FIG. 39: *Sidneioides tamaramae* — **a**, lobe of a colony (QM G9808); **b**, portion of a colony (QM G11859); **c**, zooid with ovary to right of the distal part of the rectum and embryos in atrial cavity (QM G9808); **d**, larva (AM Y1318). Scales: **a**, **b**, 5mm; **c**, 0.5mm; **d**, 0.1mm.

stigmata and up to 20 stigmata per row. Longitudinal muscles form a wide band along each side of the abdomen and posterior abdomen. Gonads are in the long, narrow posterior abdomen which is continuous with, and not constricted off from, the abdomen. The oesophagus is curved to enter the bilaterally symmetrical stomach a short way along its dorsal border. The stomach wall is smooth or it has circular mulberry-like swellings. Sometimes it is quadrate in section but it never has true longitudinal folds. The gut loop is narrow and vertical, not being twisted or horizontal as in *Polyclinum*. The male follicles are in longitudinal series (rather than being bunched) with the ovary anterior to them.

The atrial aperture is large, and often produced dorsally on a roomy siphon. The rim of the opening often has minute pointed teeth except anteriorly where it is produced into a lip. *Synoicum macroglossum* is the only species with the lip separated from the aperture. The dorso-median papilla on the body wall just behind the atrial aperture, often actually on the atrial siphon itself, occurs in most species, as it does also in *Aplidiopsis*, *Sydneioides* and in many *Polyclinum* spp. It is not a species character as Michaelsen (1930) thought it was.

Embryos usually are incubated in the postero-dorsal half of the atrial cavity, sometimes (when large) occupying the whole of the cavity. In a few species (e.g. *S. sacculum* n.sp.) the embryos are incubated in a brood pouch constricted off from the postero-dorsal corner of the thorax (rather than half-way up as in *Polyclinum*).

Larvae have median and lateral ectodermal ampullae, each with columnar ectodermal cells forming a cap over the terminal end like those of *Polyclinum*. Dorsal and ventral vesicles resemble those of *Polyclinum*, branching off epidermal strands that trail posteriorly on each side of the mid-dorsal and mid-ventral lines. In other species the vesicles are median rather than lateral and the median stems from which they branch are shorter than the lateral ones of *Polyclinum* — dorsal as well as ventral vesicles being anterior, just behind the ampullae.

In many species the branchial lobes are relatively shallow and inconspicuous (e.g. *S. bowerbanki*). In *Synoicum papilliferum* and *S. macroglossum* the atrial lips are produced from the body wall anterior to the aperture (as in the majority of *Polyclinum*). However, in other species of the genus the atrial opening is relatively primitive, with the atrial lip represented by a simple expansion of the the upper rim of the opening (as in *Polyclinum orbitum* and *Aplidiopsis*). Two or 3 lobes are on the tip of the atrial lip and other small lobes are present on the posterior rim of the opening. The condition is reminiscent of the *angolanum* group of species in *Eudistoma* (see Kott 1990) in which rudimentary cloacal systems consist of zooids arranged around shallow rudimentary cloacal cavities that are little more than depressions in the surface test (see Kott 1990). Thus the atrial aperture generally present in *Synoicum* may be a relict of an early stage in the evolution of cloacal cavities.

The presence or absence of mulberry-like swellings of the stomach wall are reliable species characters. Although these swellings are sometimes inconspicuous in small zooids, Berrill's (1950) view that the stomach is smooth in small zooids but mulberry-like in large ones is not confirmed in the present study. In certain species the stomach is large, falling into horizontal folds. Such a stomach, known from *Synoicum concavitum* n.sp. and *S. atopogaster*, resembles the stomach of *Morchellium pannosum* n.sp. and *M. albidum* n.sp. It was formerly the characteristic of the genus *Atopogaster* by which it was separated from *Synoicum*.

The curved oesophagus of *Synoicum* which usually (but not always) enters the stomach along its dorsal border, resembles that of *Polyclinum* and the Holozoinae rather than the barrel shaped, vertical and more or less radially symmetrical stomach of Diazonidae, Polycitoridae, *Ritterella* and *Aplidium*.

Synoicum rubrum (Abbott and Trason, 1968), initially assigned to *Ritterella*, apparently has closer affinities with the present genus as, despite its lack of zooid systems, it has a characteristic mulberry-like stomach with the oesophagus entering its dorsal surface.

Synoicum is cosmopolitan, known from both northern and southern hemispheres, especially in polar waters. It is well represented in Australia by indigenous species, of which the majority are temperate, although some are tropical (Table 6). It is most diverse in New Zealand waters (see Millar 1982).

Key to species of *Synoicum* recorded from Australia

1. Stigmata in 4 rows ..... *S. bowerbanki*
   Stigmata in more than 4 rows 2

2. Colony long, narrow, cylindrical stalks with zooids opening onto terminal head 3

Colony not long, narrow, cylindrical stalks with zooids opening onto terminal head 5

3. Stigmata in 9 rows; more than one system per lobe; tropical ..... *S. buccinum* n. sp.
Stigmata in more than 9 rows; one system per lobe; temperate 4

4. Stomach wall mulberry like; system stellate ..... *S. angustum* n.sp.
Stomach wall not mulberry-like; system circular ..... *S. arenaceum*

5. Stomach wall mulberry-like 6
Stomach wall not mulberry-like 8

6. Colony separate flat-topped lobes on sandy base ..... *S. sacculum* n. sp.
Colony not separate flat-topped lobes on sandy base 7

7. Colony a flat irregular sheet; surface raised into dome-like swellings over each system ..... *S. intercedens*
Colony not a flat irregular sheet; surface not raised into dome-like swellings over each system ..... *S. erectum* n. sp.

8. Atrial lip separate from aperture 9
Atrial lip not separate from aperture 10

9. Sand in layer externally; temperate ..... *S. papilliferum*
Sand not in layer externally, tropical ..... *S. macroglossum*

10. Parastigmatic vessels present .. *S. atopogaster*
Parastigmatic vessels not present 11

11. Zooids arranged in conspicuous longitudinal double row systems ..... *S. longistriatum* n.sp.
Zooids not arranged in conspicuous longitudinal double row systems 12

13. Cloacal cavities beneath deep depressions in surface 13
Cloacal cavities not beneath deep depressions in surface 16

13. Cloacal canals surround elevated zooid-free areas ..... *S. chrysanthemum* n.sp.
Cloacal canals do not surround elevated zooid-free areas 14

14. Conspicuous elevated ridges around depressions in surface ..... *S. castellatum* n.sp.
Conspicuous elevated ridges not present around depressions in surface 15

15. Stigmata up to 18 per row ..... *S. concavitum* n.sp.
Stigmata up to 12 per row ..... *S. tropicum*

16. Colony of numerous lobes on sandy base 17
Colony not numerous lobes on sandy base ..19

17. Colony lobes sandy 18
Colony lobes naked ..... *S. suarenum* n.sp.

18. Systems more than one per lobe ..... *S. durum* n.sp.
Systems one per lobe ..... *S. obscurum* n.sp.

19. Colony, flat-topped ..... *S. galei* n.sp.
Colony not flat-topped 20

20. Thorax long and narrow, about 16 rows of stigmata ..... *S. prunum*
Thorax not long and narrow, about 8 rows of stigmata ..... *S. citrum* n.sp.

Species recorded from waters adjacent to Australia

Synoicum apectetum Millar, 1982, from the northern tip of the North I. of New Zealand, has colonies resembling those of *S. buccinum* n. sp. However the New Zealand species has only one or 2 systems per colony lobe, and its atrial lip is separate from the aperture, as in *S. papilliferum.*

Synoicum haurakiensis Brewin, 1951 from the Hauraki Gulf, has a mulberry-like stomach, and the atrial lip apparently from the upper rim of the aperture. The colony is stalked and the systems are circular. The species is distinguished from *S. sacculum* n. sp. by its stalked colony.

Synoicum herdmani Brewin, 1956 from Chatham I., New Zealand has stalked lobes with circular systems. Zooids have a smooth stomach. The atrial lip appears to be independent of the aperture. The flat-topped colony may be distinctive (see below, *S. arenaceum*).

Synoicum hypurgon Michaelsen, 1924 from Hauraki Gulf, New Zealand, is not conspecific with the specimens from Fremantle which Michaelsen (1930) assigned to *S. hypurgon* as forma galei. The New Zealand colonies are club- or pear-shaped, with obscure systems, faecal pellets in the test, naked upper surface and sandy base, smooth stomach wall, atrial lip from the upper rim of the opening and a brood pouch constricted off from the body wall like *S. sacculum* n. sp. It resembles the tropical Australian *S. suarenum* n. sp., although the latter lacks a brood pouch, and has a dorsal papilla.

Synoicum kuranui Brewin, 1950b, from Great Barrier I., New Zealand, has flat-topped, sandy lobes up to 1.5cm high, reducing in diameter toward the base. The zooids, in round or oval systems, have mulberry-like stomachs. It is distinguished from *S. sacculum* n. sp. by the shape of the colonies, with their narrow sandy basal stalks. Kott (1963) assigned specimens

TABLE 6. Summary of characters of species of *Synocium* recorded from Australia

Species	Biogeographical Range[1]	Range anticlockwise around Australia	Colony	Systems	Stigmata: no. rows; no./row	Atrial lip[2]	Dorsal papilla[3]	Stomach wall[4]	Embryos: number;larval trunk median length (mm)	Other
S. bowerbanki	A,te	Fremantle – Vic.	sessile, upright with or without sand	circular	4;15	R	N	S	5;0.75	small branchial lobes
S. buccinum n.sp.	A,tr	Capricorn Gp – Coral Sea	long sandy stalks	"	9;20	"	"	"	2; 0.65	barrel-shaped stomach
S. arenaceum	Tasman Sea, te	Victoria – New Zealand	"	circular one/lobe	>13;?	"	"	"	?	
S. chrysanthemum n.sp.	A,tr	WA	stalked heads, with sand	canals circular	10;10	S	"	"	?	
S. papilliferum	A,te	Bunbury – Vic.	"	?	16–17; 9–10	"	P	"	?	
S. macroglossum	A,tr	Heron I. – NW Aust.	"	circular	18; 12–14	"	"	"	?	
S. intercedens	WP,tr	Capricorn Gp	"	"	14–17; 12–14	R	"	M	2;	
S. angustum n.sp.	A,te	Bass St	"	canals converging to terminal apertures; one/lobe	14; 20	"	"	"	?; ?	
S. erectum n.sp.	A,te	SA – Vic.	upright, sand externally	circular	12;8	"	"	"	2; 0.70	stomach areolations internal
S. sacculum n.sp.	A,te	SA – Tas	flat-topped lobes naked; sandy base	"	10;8	"	"	"	3; 0.4	brood pouch
S. obscurum n.sp.	A,te	Vic. to NSW	short, sandy lobes	circular one\lobe	20;20	"	"	I	5; 0.6	
S. suarenum n.sp.	A,tr	Capricorn Gp	flat-topped lobes naked; sandy base	circular	16;10	"	"	S	3; 0.6	
S. durum n.sp.	A,tr	Heron I.	short, sandy lobes	"	10;15	"	"	"	2; 0.45	
S. longistriatum n.sp.	A,te	Cockburn Sd	upright, sandy	canals converging to terminal apertures	16;16	R	N	S	?; ?	
S. atopogaster	A,te	WA	"	circular	17;10	"	"	"	1; 1.3	
S. tropicum	WP,tr	NW Aust.	massive, naked	circular; depressed into surface	12;8–10	"	"	"	?	
S. concavitum n.sp.	A,te	WA	"	"	15;18	"	"	"	?	
S. castellatum	A,tr	NE Aust.	"	"	22;30	"	"	I	3; 1.3	protuberant common cloacal aperture
S. prunum	A,te	NSW – Qld	"	circular, not depressed into surface	15;8	"	P	"	2; 0.56	
S. galei n.sp.	A,te	Fremantle	extensive sheets naked on upper surface	"	?	"	N	"	2;?	brood pouch
S. citrum n.sp.	A,te	SA – Tas	naked cushions	"	8; 20	"	"	"	?	

[1] A, indigenous; WP, Western Pacific; tr, tropical; te, temperate. [2] S, separate from atrial siphon; R, from rim of atrial siphon. [3] P, present; N, not present. [4] S, smooth; M, mulberry-like; I, irregular.

from Heron I. to this species, but re-examination has shown them not to be conspecific (see *Synoicum durum* n. sp.). Other colonies assigned to this species from Fiji (Kott 1981) and Indonesia (*S.? clavatum*: Millar, 1975) appear to be colonies of *S. suarenum* n. sp.

Other species from the South I. of New Zealand (see Millar 1982) not likely to occur in Australia, are *S. stewartense* (Michaelsen, 1924), *S. pererratum* (Sluiter, 1912), *S. otagoensis* Millar, 1982 and *S. occidentalis* Millar, 1982.

Synoicum angustum n.sp.
(Fig. 40a,b)

DISTRIBUTION

TYPE LOCALITY: Tasmania (45 nautical mls NNE of East Sister Is, 39°00'S 148°25'E, 92m sandy bottom, epibenthic sled CSIRO *Soela* Statn 22, coll. W. Zeidler 14.10.84, holotype SAM E2570, paratypes SAM E2572 E2573.

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are almost spherical heads (about 1cm diameter) on the terminal free ends of narrow branching sandy stalks about 6cm long and 0.5cm diameter. Zooids are in double rows along the sides of the head converging to a terminal, sessile common cloacal aperture. Sand adheres to the head to form a light covering but a thick coat of sand is crowded on the stalk. Sand is not embedded internally.

In preservative the zooids are reddish, and these, showing through the translucent test and the light covering of sand, make the head appear as brownish-red. The colour of the living colony is not known.

INTERNAL STRUCTURE: Zooids are robust when contracted, but only about 4mm long, the thorax and abdomen of equal length and together about half the length of the zooid. When extended it is probable that they are thread-like and extend down into the stalk. The rim of the branchial aperture is divided into 6 rounded lobes, and the atrial aperture has a moderately long, pointed, fleshy lip from the upper border of the opening. A median dorsal papilla behind the lower rim of the atrial aperture is a flat tongue-like projection or flap bent anteriorly or posteriorly against the zooid. Ten longitudinal muscles are on the thorax and extend down the rest of the zooids as a ventral band. About 14 rows of stigmata have 20 or more stigmata per row. These could not be counted accurately owing to the contracted thorax. The oesophagus and post-pyloric part of the gut loop are long. The stomach has rounded swellings in its wall to give a mulberry-like appearance.

The posterior abdomen has a moderately long sometimes branched terminal vascular appendix. Neither mature gonads nor embryos are present in this type material.

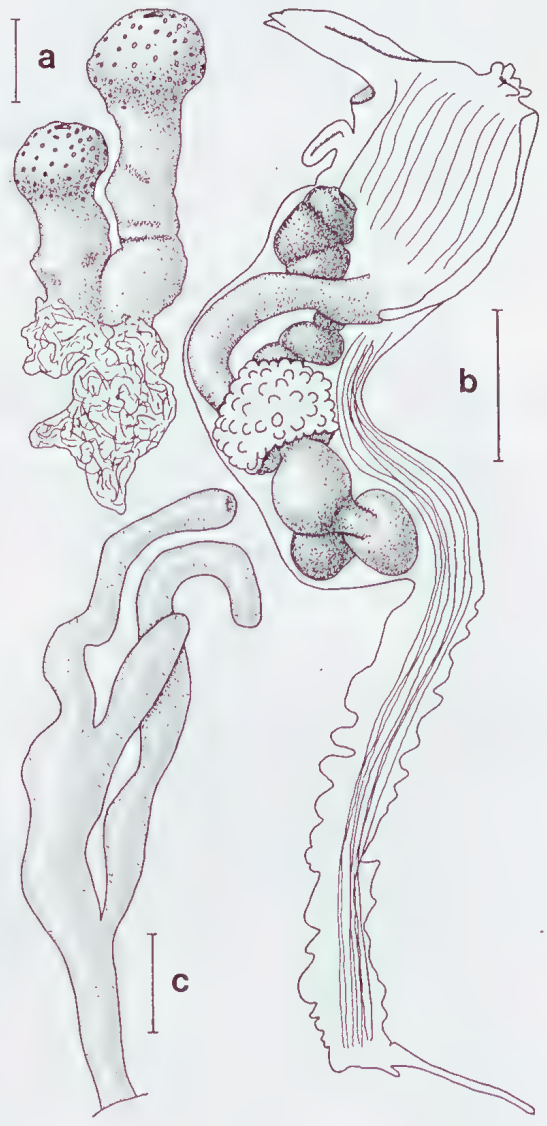


FIG. 40: *Synoicum angustum* n.sp. — **a**, colony (paratype SAM E2572); **b**, zooid (holotype SAM E2570). *Synoicum arenaceum* — **c**, colony (MV F58686). Scales: **a**, 5mm; **b**, 1mm; **c**, 1cm.

REMARKS

This species has the same mulberry-like stomach and the same temperate ranges as *S. sacculum* n.sp., from which it is distinguished by the long, narrow branching stalks of its small but distinctive colonies and its long posterior abdomen. The colonies of other stalked species of this genus, viz. the tropical *S. buccinum* n.sp., and the temperate *S. arenaceum* are distinguished by their circular (rather than radiating double-row) systems and smooth stomach walls. *Synoicum erectum* n.sp. also has a mulberry-like stomach and naked heads on a sandy base. However a number of circular systems opening on the upper surface of *S. erectum* and narrower thoraces with only about 8 stigmata per row distinguishes it from the present species. The flap-like dorsal papilla is also unique, distinguishing *S. angustum* from all others is this genus.

Synoicum arenaceum (Michaelsen, 1924)
(Fig. 40c)

Macroclinum arenaceum Michaelsen, 1924, p.406,
Synoicum arenaceum: Millar, 1960, p. 361; 1982, p.21.

DISTRIBUTION

NEW RECORD: Victoria (off Cape Howe, MV F58686).
PREVIOUSLY RECORDED: ? Victoria (Port Phillip Bay — Millar 1960). New Zealand, Stewart I. (Michaelsen 1924). The new record is from 274m.

DESCRIPTION

EXTERNAL APPEARANCE: The newly recorded specimen is a narrow, cylindrical branching stalk, branching twice, and about 6cm long overall. The terminal branches are about 4mm diameter. Each branch occupies about one third of the total length. The tip of each terminal branch is naked, about the same diameter as the rest of the stalk, with a central sessile cloacal aperture around which the zooids appear to be arranged. The remainder of the colony is covered with sand, and also sand is embedded internally.

INTERNAL STRUCTURE: The zooids in this specimen are muscular and very contracted and few details of their morphology can be determined. The atrial lip is produced from the rim of the atrial aperture. There are at least 13 rows of stigmata. The large smooth-walled stomach is halfway down the abdomen. Gonads are not mature.

REMARKS

The identification of this specimen is based on the form of the colony. However the free end of the head is expanded and flat in the type specimen, but not in the present specimen. Millar (1966) did not describe the specimen he recorded from Port Phillip Bay. Kott (1969) thought this species to be synonymous with the sub-antarctic *A. recumbens*; and Millar (1982) referred to proposals that *S. arenaceum, S. herdmani* and *S. kuranui* are conspecific. Generally the relationships of these species are unresolved, although *S. kuranui* unlike the others has a mulberry-like stomach, and appears to be different. Further, colonies of the present species have long cylindrical branching stalks different from the tapering ones of *S. kuranui*. At this stage the New Zealand populations require review, and more Australian material is needed to establish the status of this species and its populations on both sides of the Tasman Sea.

Synoicum atopogaster Kott, 1963
(Fig. 41)

Synoicum atopogaster Kott, 1963, p.89.

DISTRIBUTION

NEW RECORDS: None.
PREVIOUSLY RECORDED: Western Australia (W of the Abrolhos — AM U3927 holotype Kott 1963).

DESCRIPTION

EXTERNAL APPEARANCE: The colony is a thick, cylindrical upright lobe, 5cm high and 2.5cm in diameter. A few smaller lobes are present around the base. The test of the lower half of the colony is firm, while that of the upper half is soft. A crowded layer of sand adheres to the surface test of the lower half, and some is on the upper surface between bare patches.

Zooids extend out to occupy the whole length of the colony, but when contracted they are found either near the top, or withdrawn down into the base. They are arranged in 4 or 5 systems opening around the upper surface. Each common cloacal aperture appears to be surrounded by a circle of zooids, with their branchial apertures protected by a ridge of surface test.

The holotype colony is wrinkled transversely and its head is displaced laterally.

INTERNAL STRUCTURE: The zooids are large, the thorax and abdomen of contracted zooids being at least 4mm long. They have about 30 longitudinal muscle bands on the thorax and these continue as a wide band along the ventral surface of the abdomen and posterior abdomen. When

contracted, this muscle band draws up the posterior abdomen alongside the abdomen. The branchial aperture is on a short, narrow siphon with the rim divided into 6 lobes. The 2 ventral lobes are slightly enlarged and dorsally-directed. The atrial aperture has a fleshy lip from the anterior rim and a few irregular lobes on the posterior rim.

Each of the 17 rows of up to 10 stigmata is crossed by a parastigmatic vessel, and both primary transverse and parastigmatic vessels have a dorsal languet. Transverse vessels contain muscle fibres. The oesophagus is long, the stomach voluminous, collapsed into transverse folds. The duodenum and mid-intestine are relatively long and narrow and the oval posterior stomach large.

The gonads consist of a clump of male follicles about halfway down the posterior abdomen, with a small ovary anterior to them. The vasa efferentia join to form the vas deferens about halfway up the side of the male follicles, rather than each follicle separately joining the vas deferens as it passes up the length of the posterior abdomen.

A single embryo is present in the atrial cavity of zooids of the holotype colony. The larval trunk is 1.3mm long. A median ampulla with 2 or 3 branches is in each interspace between the median adhesive organs. Minute epidermal vesicles branch off the epidermis and lie in the thin layer of test that surrounds the large trunk. The yolk mass is large, the developing adult organs are crowded into the posterior end of the trunk.

REMARKS

The zooids of this species are, in some respects,

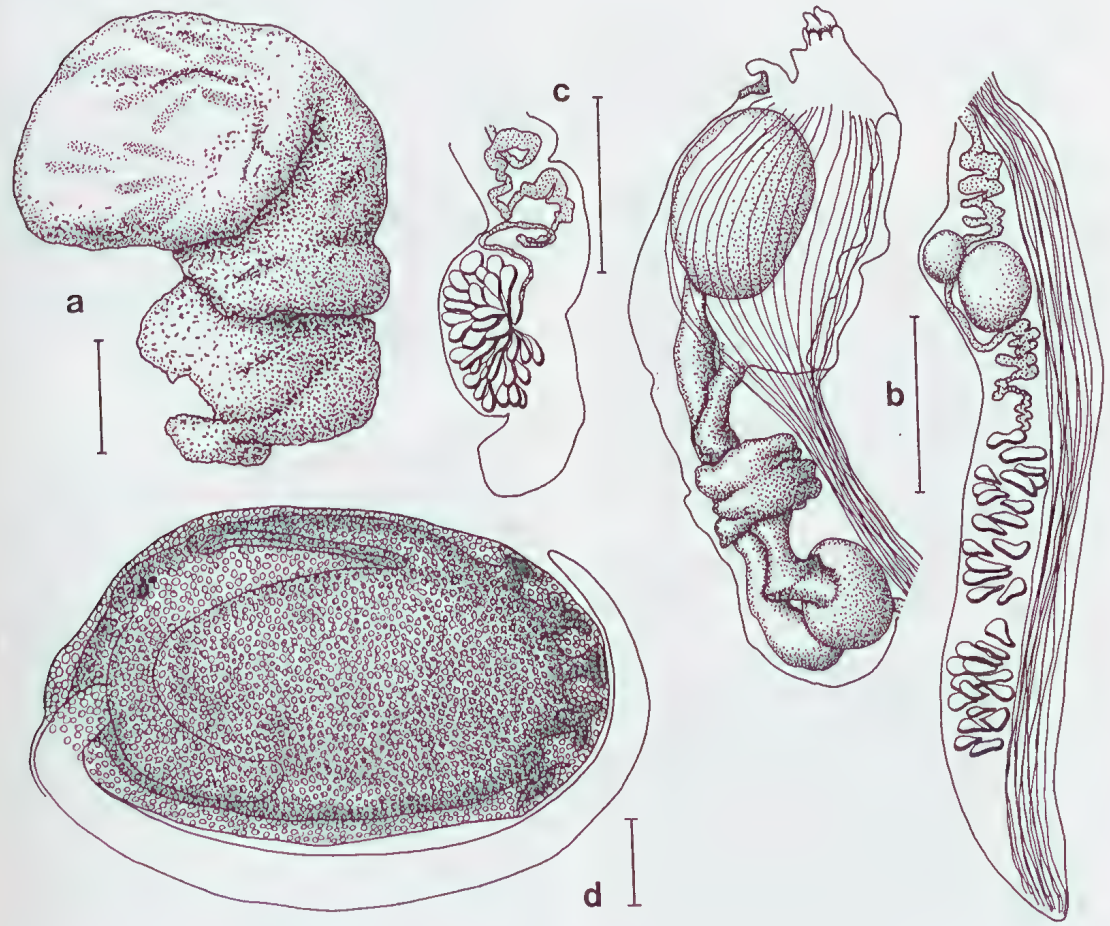


FIG. 41: *Synoicum atopogaster* (holotype AM U3927) — **a**, colony; **b**, zooid; **c**, contracted posterior abdomen; **d**, larva. The epidermal vesicles in the test around the sides of the larval trunk are not shown. Scales: **a**, 1cm; **b**, **c**, 1mm; **d**, 0.2mm.

like those of *S. concavitum* n.sp., having a similar large stomach, a strong ventral muscle, and conspicuous transverse muscles in the branchial sac. However, *S. concavitum* n.sp., has a flat rather than upright colony with more numerous, but smaller systems in firm, naked, gelatinous test.

The relationship of the species to *Morchellium pannosum* n.sp. is discussed below. The course of the vas deferens resembles that of *Pseudodistoma candens* n.sp., but a phylogenetic relationship between these taxa is not implied.

Synoicum bowerbanki Millar, 1963
(Fig. 42. Plate 8a)

Synoicum bowerbanki Millar, 1963, p.697.

DISTRIBUTION
NEW RECORDS: Victoria (Portland, QM GH38, SAM E2551, MV F59372).
PREVIOUSLY RECORDED: Western Australia (Fremantle — Millar 1963). Millar (1963) records a further specimen from an unknown Australian locality.

DESCRIPTION
EXTERNAL APPEARANCE: Colonies are upright and club-shaped (to 6cm high) to almost spherical (to 5cm in diameter). A short stalk from the under surface reduces in diameter toward the substrate, although in some specimens it is divided into branched roots. Several of the newly recorded specimens (SAM E2551, QM GH38) have a single layer of sand grains attached to the surface test, interrupted over the zooid openings. Several upright, club-shaped colonies (MV F59372), however, are naked with basal sandy roots. Sand is not present internally.

Zooids are arranged in evenly spaced circular cloacal systems of about 6 zooids around a central cloacal aperture. Each system is about 5mm in diameter.

The red test of living colonies becomes transparent and pink in preservative, although this is obscured by the surface layer of dark grey sand grains. The naked colonies are opaque purple on the surface, but transparent internally. The test is gelatinous and firm, but soft.

INTERNAL STRUCTURE: Zooids are long (to 1cm) and thread-like. When contracted, the thorax and abdomen together are about one third of the total length. The terminal branchial aperture is almost smooth-rimmed, the 6 branchial lobes being almost completely suppressed. The atrial aperture is on a relatively long siphon, with its anterior border produced into a lip with its tip divided into 3 rounded lobes which are inserted into the rim of the cloacal aperture. Apart from the sphincter muscles around the apertures, thoracic musculature is limited to about 14 fine longitudinal and oblique muscles. These extend in a band along each side of the abdomen and posterior abdomen. There are 4 rows of stigmata with up to 15 per row. The oesophagus is curved, the stomach wall is smooth. The duodenal part of the gut is long and the mid-intestine is expanded before opening into an oval posterior stomach in the bend of the gut loop. The anal opening is about one-third of the way up the thorax.

A group of 3 or 4 oocytes are posterior to a gonad-free part of the posterior abdomen behind the gut loop. Behind the ovary are testis follicles in a single longitudinal series sometimes occupying most of the length of the posterior abdomen. The testis follicles are spent in the colonies with embryos being incubated. The species may be protandrous.

Zooids of colonies collected in July (QM GH38) have up to 5 embryos at a time in the atrial cavity. They are at different stages of development, and perhaps were fertilised in the oviduct. Larvae have a trunk 0.7mm long. Small adhesive organs on slender stalks alternate with conical median ampullae. There also are 4 rounded lateral ampullae on each side. Ampullary vesicles develop on a posteriorly projecting median stalk both ventrally and dorsally. The larval tail reaches to the anterior end of the trunk.

REMARKS
The holotype of this species from Fremantle (Millar 1963) and the specimens Millar described at the same time, from an unknown locality, are fleshy naked masses, up to 9cm in maximum extent, and 3cm thick. Most of the newly recorded specimens have a single layer of sand adhering to the surface test, although some club-shaped ones from Portland (MV F59372) are naked, but with sandy basal root-like projections of the test. However, all known specimens have an almost smooth branchial aperture, a conspicuous atrial siphon with a tridentate tip on the anterior lip, smooth stomach wall, a single row of male follicles, 4 rows of up to 15 stigmata, and a similar larva. Although the cloacal systems of the type specimens are not described, the unusual almost smooth branchial apertures together with the reduced branchial sac support the view that the newly recorded material from south-eastern Australia (in which there is some variability in shape and in the presence of a surface layer of sand) is

conspecific with the type specimens (Millar 1963).

The oesophagus of *Synoicum* spp. is characteristically longer than in most other genera of the Polyclinidae, and its curve is also characteristic of the genus. However, the oesophagus of the type specimen of *S. bowerbanki* figured by Millar (1963, p.697) is unusually long in relation to the total length of the gut loop, the stomach being in the posterior third of the abdomen rather than half way down it as is more usual.

Synoicum buccinum n. sp.
(Fig. 43. Plate 8b)

DISTRIBUTION

TYPE LOCALITY: Coral Sea (Marion Reef, cave, 8m, coll. N. Coleman 24.8.77 AMPI 209, holotype QM GH5045). Queensland (Heron I., rubble zone, sandy substrate, coll. P. Kott 26.2.84, paratypes QM GH5046; W. reef crest, W. Wistari Reef, coll. P. Kott 12.9.84, paratypes QM GH5047; NW corner Wistari Reef, coll. P. Kott 3.11.86, paratypes QM GH5048).

FURTHER RECORDS: Queensland (Capricorn Group, QM GH5049–52 GH5585).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are slender, sandy, cylindrical, irregularly bent, branching stalks. The terminal branches are about 1cm long and 3mm in diameter expanding toward the free end into a rounded to flat-topped or flattened mushroom-like naked head up to 1.5cm in diameter onto which the zooids open. Each terminal

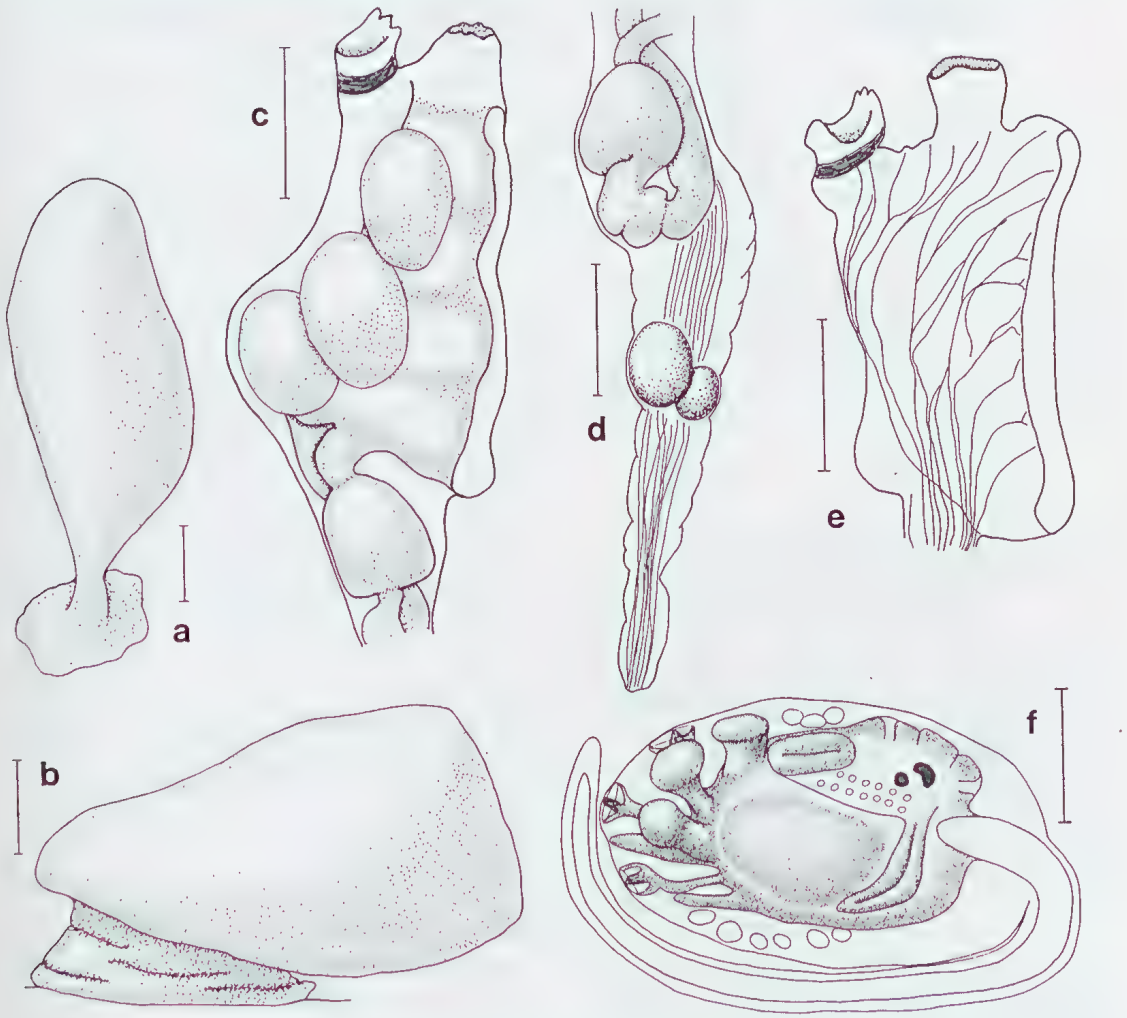


FIG. 42: *Synoicum bowerbanki* — **a**, **b**, outline of colonies (MV F59372, QM GH38); **c–e**, parts of zooids (QM GH38); **f**, larva (QM GH38). Scales: **a**, **b**, 1cm; **c–e**, 0.5mm; **f**, 0.2mm.

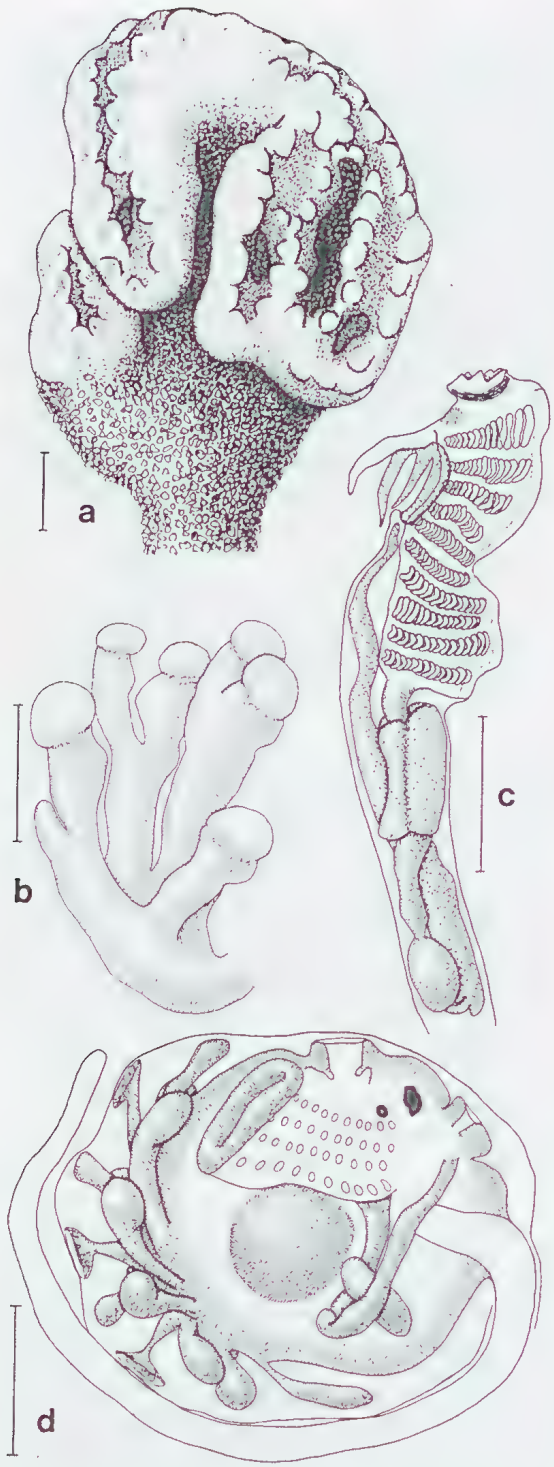


FIG. 43: *Synoicum buccinum* n.sp. — **a**, **b**, colonies (**a**, detail of systems, paratype QM GH5048; **b**, outline of holotype QM GH5045); **c**, thorax and abdomen (QM GH5299); **d**, larva (paratype QM GH5047). Scales: **a**, 2mm; **b**, 1cm; **c**, 0.5mm; **d**, 0.2mm.

stalk contains from one to 5 or 6 circular to long systems of 6 or more zooids around large, sessile common cloacal apertures. The systems often are separated from one another by deep furrows in the surface test.

Sand is on the external surface of, and embedded through, the stalk, making it hard, but not brittle. The sand sometimes projects up into the centre of the head and forms partitions around the systems. It is always absent from around the zooids in the soft, upper layer of translucent test, through which the zooids can be seen perpendicular to the terminal surface. Sometimes green algal cells are embedded in the surface test together with a scattering of sand particles.

In life the head is 'orange buff' or 'orange rufus' with zooids 'orange chrome' (Ridgeway 1886), but the sandy stalk has no colour and usually is embedded in the substrate.

INTERNAL STRUCTURE: Zooids are moderately small, the thorax and abdomen together being about 2mm long. The posterior abdomen is very long, projecting down into the stalk. One or 2 stolonic vessels are at the posterior end of the posterior abdomen. About 6 fine longitudinal muscle bands extend the whole length of the zooid. The atrial apertures are wide and sessile, with a frilled margin. Muscles are present around the sides and posterior rim of the aperture, and the outside ones loop back across the postero-dorsal surface of the body. The atrial aperture can probably be closed by contraction of the muscles around it, but in most of the zooids examined the dorsal border of the zooid is contracted and concave, partially occluding the aperture. The anterior rim of the atrial aperture is produced into one to 3 long, pointed lips. Nine rows of stigmata are in the pharynx, with 16 per row posteriorly, and 20 per row anteriorly. The gut loop is vertical, and the oesophagus relatively straight. The smooth-walled stomach is quadrate in section and sometimes appears to have 4 folds. These are not true folds. The duodenal area is moderately long, and a posterior stomach is in the bend of the gut loop.

Two rows of male follicles are in the posterior half of the posterior abdomen of the holotype and a small ovary is anterior to the male follicles. A single embryo is in the atrial cavity of this specimen lot (collected in August). Two embryos, one an advanced tailed larva, are present in specimens collected in September. Larvae have an almost spherical trunk about 0.65mm long with the tail wound about three quarters of the way around it. There are median and lateral ampullae, but epi-

dermal vesicles were not detected in the larval test. Both otolith and ocellus are present.

REMARKS

The straight oesophagus and more or less barrel-shaped stomach of this species approach the condition found in *Aplidium* spp. However, stomach folds, when they occasionally are found, do not appear to be structural and the stomach generally is smooth, justifying its position as a species of *Synoicum*.

The colonies resemble those of *S. arenaceum* Michaelsen, 1924 and *S. apectetum* Millar, 1982, from temperate New Zealand waters. The species is distinguished from both by the numerous systems in each head, and further distinguished from Millar's species by the origin of the atrial lip from the rim of the aperture (rather than separately from the body wall anterior to the opening), and by the length of the larval trunk (only 0.5mm in Millar's species). *Synoicum arenaceum* is also distinguished by its more numerous rows of stigmata.

Synoicum castellatum n.sp.
(Fig. 44. Plate 8c–e)

DISTRIBUTION

TYPE LOCALITY: Queensland (Heron I, North Point, 5m, coll. D. Parry 4.11.86, holotype QM GH5160; coll. R. Day 4.7.73, paratypes QM GH5163).

FURTHER RECORDS: Western Australia (Exmouth Gulf, QM GH5401). Queensland (Capricorn Group, QM GH5161–2 GH5164–5 GH5512 GH5587 GH5590; Swain Reefs, AM Roche ZQ 326; Broadhurst Reef, QM GH5351 GH5503; Whitsunday Is, QM GH5508; Hook and Hardy Reefs Channel QM GH5376 GH5509; Lizard I., QM GH5332; Raine I., QM GH5627). Northern Territory (Gulf of Carpentaria, AMY1062).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are robust, usually massive cushions to 10cm diameter and about 2cm high. The upper surface has raised rounded ridges that surround more or less circular to irregularly shaped, or stellate depressions. A conical cloacal aperture protrudes from the centre of each depression rising above the level of the rounded ridges. The branchial apertures are around each depression at the base of the raised ridges. A shallow but extensive cloacal cavity surrounded by the zooids is beneath each depressed area. The test is translucent, firm and gelatinous. In life colonies are 'fleshy' coloured, with 'isabella' colour (Ridgeway 1886) in the centre of the ridges. In preservative the flesh colour becomes beige, some darker grey along the ridges and in the margins of the colony, and minute dark pigment cells in the test.

The zooids are in rigid compartments in the firm test. They are large and not crowded. Neither embedded nor adherent sand is present.

INTERNAL STRUCTURE: Zooids are large and robust, the thorax and abdomen together about 1cm, even in contracted zooids. The posterior abdomen is at least twice that length. Each branchial aperture has 6 large triangular lobes and a strong sphincter muscle behind the branchial lobes. The atrial tongue is fleshy, sometimes long and pointed, sometimes contracted and blunt and occasionally divided into 2 lobes. Five small pointed papillae are evenly spaced around the rim of the atrial aperture posterior to the atrial tongue, which extends out from the anterior rim of the opening. About 30 longitudinal muscles are in the parietal wall of the thorax, and these continue along the length of the zooid. Transverse muscles are in the transverse vessels of the branchial sac. Short stumpy connecting branches from the muscles in each transverse vessel cross the atrial cavity in connecting vessels about one third of the distance from the dorsal mid-line. These muscles break into terminal branches which join with the eighth to tenth longitudinal muscles on each side of the pharynx. The connecting vessels with their contained muscles effectively divide the atrial cavity into a dorsal chamber (containing faeces and embryos) and a ventral chamber on each side of the pharynx.

The branchial sac is long and wide with 18 to 22 rows of stigmata. In the centre of the sac about 30 stigmata are in each row but the rows dramatically reduce in length posteriorly.

The stomach is large, and its shape sometimes is obscured by horizontal folds when contracted. The stomach wall is smooth externally in the relaxed zooid, but with some variability in its internal lining. Occasionally vertical divisions separate the glandular lining into 4 to 8 ribbon-like bands. In other specimens these bands become irregular patches of glandular epithelium interrupted by branching internal ridges which may be parallel to one another toward the posterior end of the stomach. The remainder of the descending limb of the gut loop has the usual duodenum, proximal part of the mid-intestine, small posterior stomach, and the distal part of the mid-intestine which opens into the rectum at the base of the ascending limb of the gut loop. The

anus is trumpet-shaped and circular. It is not divided into 2 lips. A few relatively large oocytes are anterior to 2 irregular, crowded series of more or less club-shaped testis follicles, in the posterior half of the long, cylindrical posterior abdomen.

One to 3 large embryos are being incubated in the dorsal peribranchial cavity of zooids collected at Heron I. in June and July, but not in August, September or November. Larvae have a trunk 1.0mm long, with the tail wound three-quarters of the distance around it. Median ampullae alternate with the 3 narrow-stalked, shallow adhesive organs. Bands of crowded epidermal vesicles are crowded across the dorsal and ventral mid-lines behind the adhesive organs and extend anteriorly along each side of the mid-line.

Remarks

These large, robust, naked colonies with their zooid systems opening into large depressed areas separated by high rounded ridges of naked test, superficially resemble both *Lissoclinum patella* (Didemnidae: see Kott 1980) and *Aplidium crateriferum* (see below). The large, protuberant

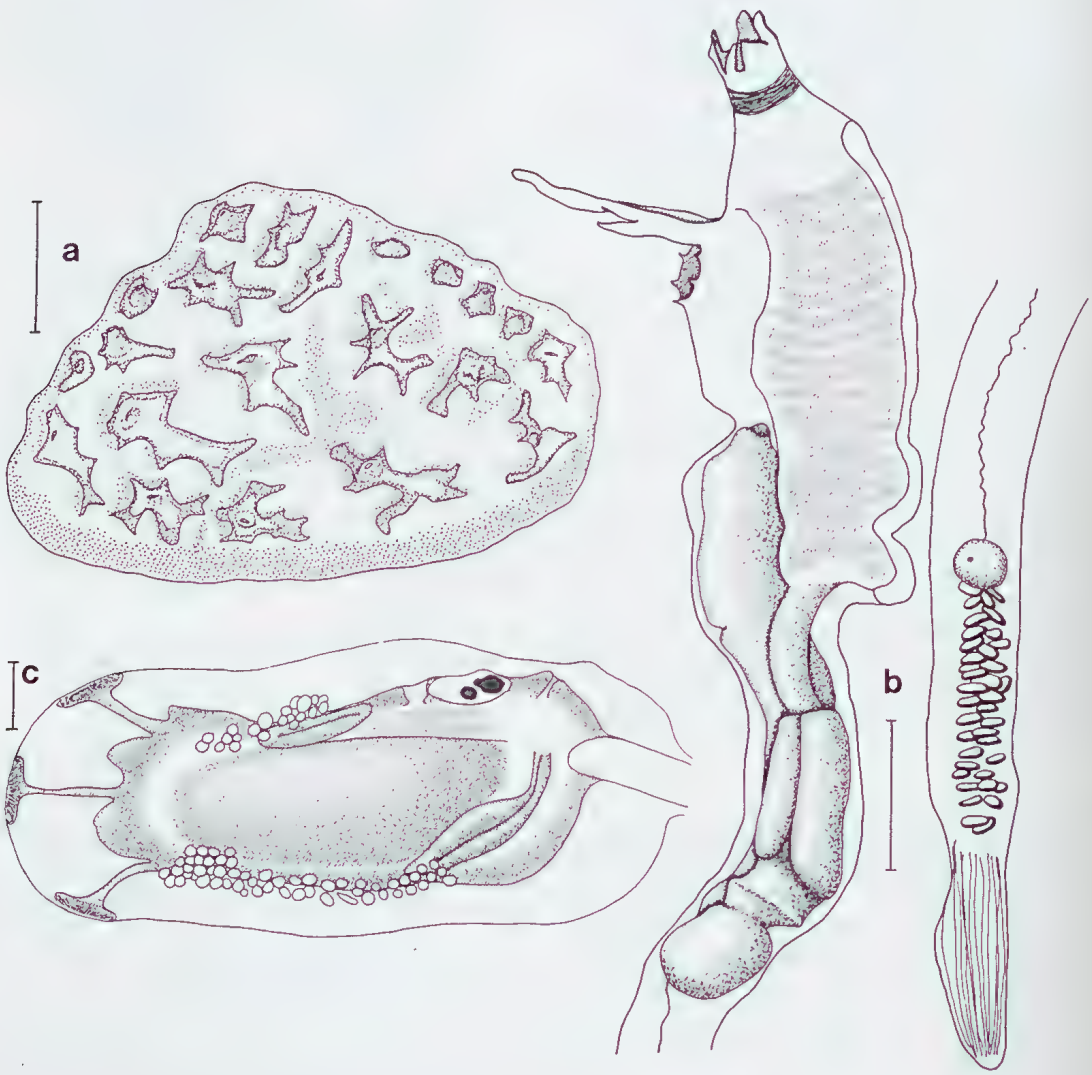


FIG. 44: *Synoicum castellatum* n.sp. — **a**, colony (holoytpe QM GH5160); **b**, zooid (QM GH5164); **c**, larva (QM GH5163). Scales: **a**, 2cm; **b**, 1mm; **c**, 0.1mm.

common cloacal apertures of the latter also resemble those of the present species. In addition to the differences in its stomach wall, *A. crateriferum* systems open into depressions that are long, slightly curved with excentric cloacal apertures rather than the more circular to stellate depressions with central common cloacal that occur in the present species. *Aplidium crateriferum* also has a differently shaped zooid from that of the present species, with the atrial lip separated from the aperture and a narrow thorax with only 8 (rather than the present 30 stigmata).

Aplidium clivosum n.sp. has a similar robust colony, but the zooids are in double rows along cloacal canals that converge to the common cloacal apertures.

Synoicum chrysanthemum n. sp.
(Fig. 45)

DISTRIBUTION

TYPE LOCALITY: Western Australia (NW Bluff Point 27°40'S 113°03'E, 130m, CSIRO 22.8.63, holotype WAM 1031.83; paratype 21.8.63 WAM 1032.83; 80km W of Dongara 64m, MV Sprightly 19.2.76, paratype WAM 850.83 *QM GH2115*).

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are mushroom-like consisting of a spherical to conical head to 5cm in diameter, on a thick, cylindrical stalk 3 to 4cm long and 1cm in diameter. Basally the stalk divides into 2 or 3 short thick roots.

The preserved colonies are opaque and white. Sand is crowded in the surface layer of test, but becomes less so internally. The surface of the head is covered with circular zooid-free areas (about 5mm in diameter) which swell out from the surface a little. These are surrounded by cloacal canals which lie beneath depressions or creases in the surface test. The layer of test over the cloacal canals is thin but opaque with sand embedded. Common cloacal cavities are where several of the circular canals meet beneath a large common cloacal aperture. Cloacal canals are rigid with sand and in the examined colonies the branchial sacs are exposed directly to them through the large atrial apertures.

INTERNAL STRUCTURE: The thorax and abdomen together are about 3mm long, with the thorax longer than the abdomen. The posterior abdomen

FIG. 45: *Synoicum chrysanthemum* n.sp. (paratype QM GH2115) — a, colony; b, relaxed zooid with wide open atrial aperture. Scales: a, 2cm; b, 0.5mm.

is particularly long, extending into the centre of the head and down into the stalk.

One to 3 shallow to pointed, fleshy atrial lips are produced from the body wall just anterior to the atrial sphincters. The atrial aperture is open for about the middle two-thirds of the length of the thorax. No dorsal papilla was seen, although its presence could have been obscured by the wide open atrial aperture. About 10 rows of 10 long narrow stigmata are in the branchial sac. The stomach is smooth, and quadrate in section. Gonads were not observed in the examined material.

REMARKS

The organisation of the cloacal systems, with zooids in double rows, one row along each side of the narrow canals that surround the raised circular areas on the surface, resembles some *Aplidium* species (e.g. *A. tabascum* n.sp., *A. cellis* Monniot, 1987) from the tropical western Pacific. The present species is stalked, unlike the sessile sheets of these *Aplidium* spp. It is further distinguished by the sand which is crowded throughout the test.

Synoicum citrum n. sp.
(Fig. 46. Plate 8f)

DISTRIBUTION

TYPE LOCALITY: Victoria (Wilson's Promontory, Waterloo Bay, 25m vertical face, coll. J.E. Watson 26.1.78, holotype QM GH 5104). Tasmania (Satellite I. off Bruny I., d'Entrecasteaux Channel, 6m vertical face, coll. J.E. Watson 18.2.72, paratype MV F59369).
FURTHER RECORDS: South Australia (Port MacDonnell, QM5104 GH2294). Tasmania (Satellite I. off Bruny I., MV F59366).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are rounded, cushion-shaped, sessile and fixed by a small part of the basal surface. The test is gelatinous and translucent. The zooids open onto the upper surface. The known colonies are squashed, often mutilated. Zooids are crowded. They may be arranged in circular systems but these are obscure. The colonies are up to 2cm high and up to 3cm in maximum dimension. Zooids are said to have been bright yellow in a yellow matrix when alive.

INTERNAL STRUCTURE: Contracted zooids are nearly 5mm long, the fleshy thorax and abdomen together being about half of the total length. The thorax is especially large, with 12 to 20 longitudinal muscle bands that extend the length of the zooids. Conspicuous sphincters are present around the base of the branchial siphon. The branchial lobes are relatively low and rounded. The atrial lip, continuous with the anterior rim of the aperture, is fleshy and usually bilabiate, with each lobe long and pointed.

Seven or 8 rows of about 20 stigmata are in the branchial sac. The stomach is large almost spherical and smooth walled. Long double rows of male follicles are in the relatively short posterior abdomen.

REMARKS

The species is distinguished by its fleshy, ses-

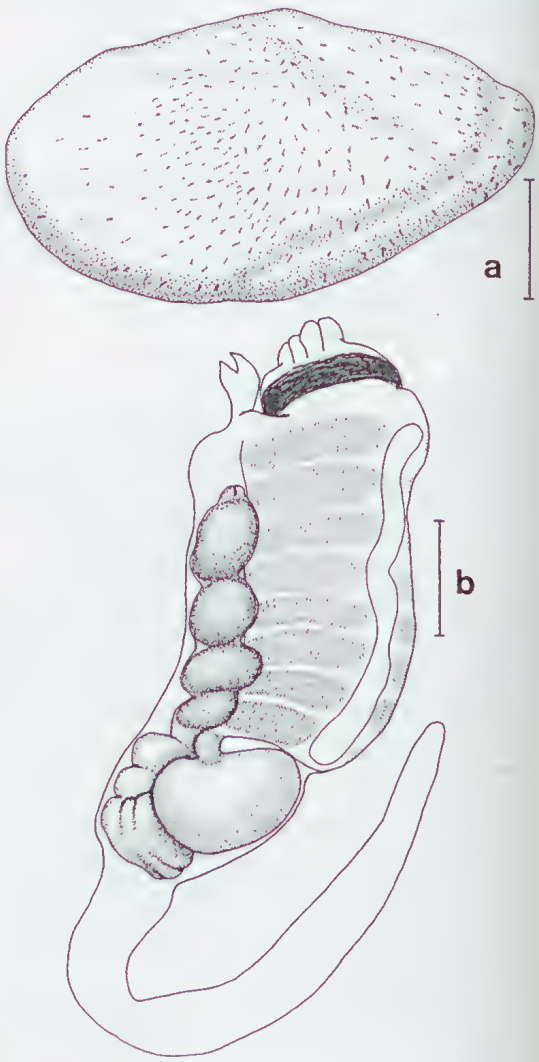


FIG. 46: *Synoicum citrum* n.sp. (holotype QM GH5014) — a, colony; b, zooid. Scales: a, 1cm; b, 0.5mm.

sile, cushion-shaped, translucent, greenish-yellow colony, which lacks sand either on the outside or embedded in the test. Zooids are relatively large for this genus, but they have fewer rows of stigmata than most other species. *Synoicum prunum*, which has a range on the mid- to north-eastern Australian coast, also has firm gelatinous colonies but the known ones are larger than the present species, and the zooids are smaller, with narrow thoraces.

Many species of this genus known *in situ* have red colonies, often with red zooids, rather than the yellowish colour of the present one.

Synoicum concavitum n.sp.
(Fig. 47. Plate 8g)

DISTRIBUTION

TYPE LOCALITY: Western Australia (Eclipse I. SW entrance to King George Sound, rocky granitic reef, large boulders, coll. AIMS Bioactivity Group 26.3.89, holotype QM GH5465).

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: The colony is an irregular cushion about 6cm in maximum dimension and up to 3cm thick. The test is firm, gelatinous, and slightly translucent. It is orange in life, but brown in preservative. Sand is on the under surface and sides of the colony, but the upper surface is naked and even. Sand is absent from the upper (thoracic) layer of test but is sparsely but evenly scattered through the lower part of the colony. The upper surface of the colony is depressed over the circular cloacal cavities. Branchial apertures of the zooids (about 12) in each system open around the perimeter of each depression. The ventral lobes of each branchial aperture extend horizontally directing the openings toward the large, protuberant cloacal aperture that rises from the centre of each depression.

INTERNAL STRUCTURE: Zooids are brown in preservative. They are large, the thorax and abdomen of about equal length, and together about 3mm long even when contracted. The branchial siphon is moderately long, with 6 pointed lobes, the ventral ones usually longer than the dorsal ones (see above). The atrial siphon, also protruding, has 3 small pointed lobes around its posterior rim, and a long strap-like tongue from the upper rim of the opening. This tongue has a straight tip with small denticulations on it.

A large number of fine longitudinal muscle bands are on the thorax, making an almost con-

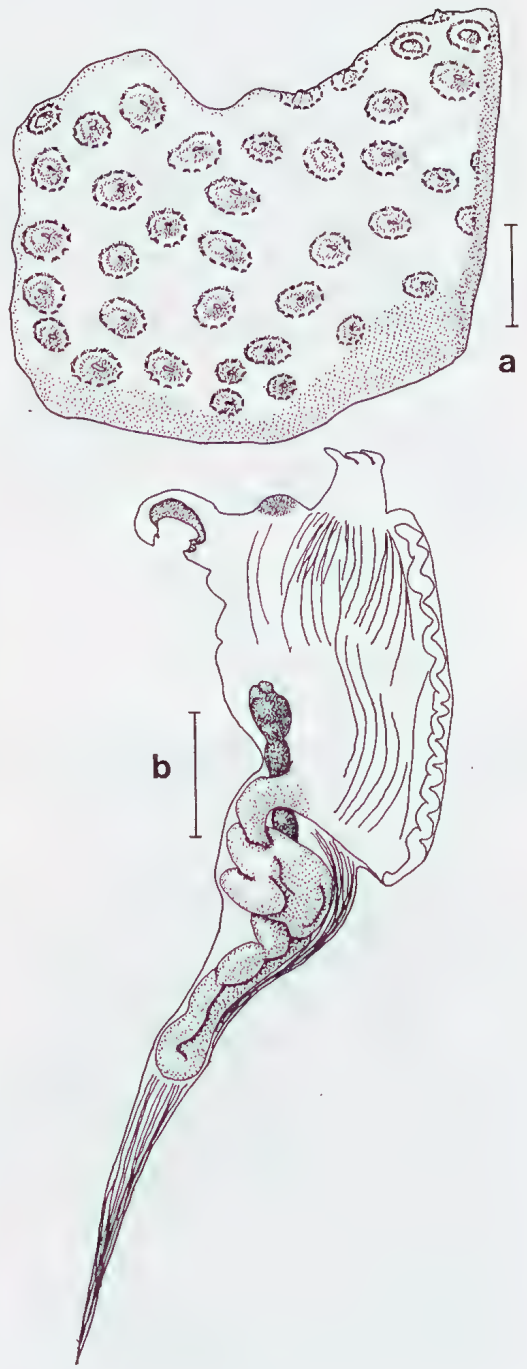


FIG. 47: *Synoicum concavitum* n.sp. (holotype QM GH5465) — a, part of colony from above; b, zooid. Scales: a, 1cm; b, 0.5mm.

tinuous coat. These extend in a band along the ventrum of the abdomen and along both sides of the posterior abdomen. Transverse muscles are in the transverse vessels. The pharynx is wide, with 15 rows of stigmata with up to 18 per row. The gut loop is moderately long, with the large, voluminous stomach about halfway down the abdomen. The stomach wall is smooth, although in these specimens it often is collapsed into irregular or horizontal folds. The duodenum and proximal part of the mid-intestine are long, and almost continuous. There is an oval posterior stomach at the base descending limb of the gut loop. The posterior abdomen is relatively short and tapering in these zooids. Gonads are not developed.

REMARKS

The species resembles *Synoicum tropicum* in the form of its systems. It is distinguished principally by the larger branchial sac of the present species.

Synoicum durum n.sp.
(Fig. 48)

Synoicum kuranui: Kott, 1963, p.88.

DISTRIBUTION

TYPE LOCALITY: Queensland (Heron I., low tide, coll. R. Carson June 1961, holotype AM U3990).

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: Small wedge-shaped to inverted conical lobes, reducing in diameter toward the base, to 1cm high and 0.8cm diameter across the flat upper surface. Sand is in a surface layer around the sides of the lobes, and on the upper surface and internal test between the systems. Two to 4 circular systems, each of up to 10 zooids, open on the flat top of each of the lobes, and sand is absent from the surface above these systems. Each system has a central sessile common cloaca. At first the test is yellowish in preservative and zooids are red, but subsequently all colour is lost.

INTERNAL STRUCTURE: The zooids are small, up to 2mm long, of which the thorax and abdomen is about half. Ten longitudinal muscles are on each side of the thorax, and these extend in a wide band along each side of the abdomen and posterior abdomen. The branchial siphon is short and

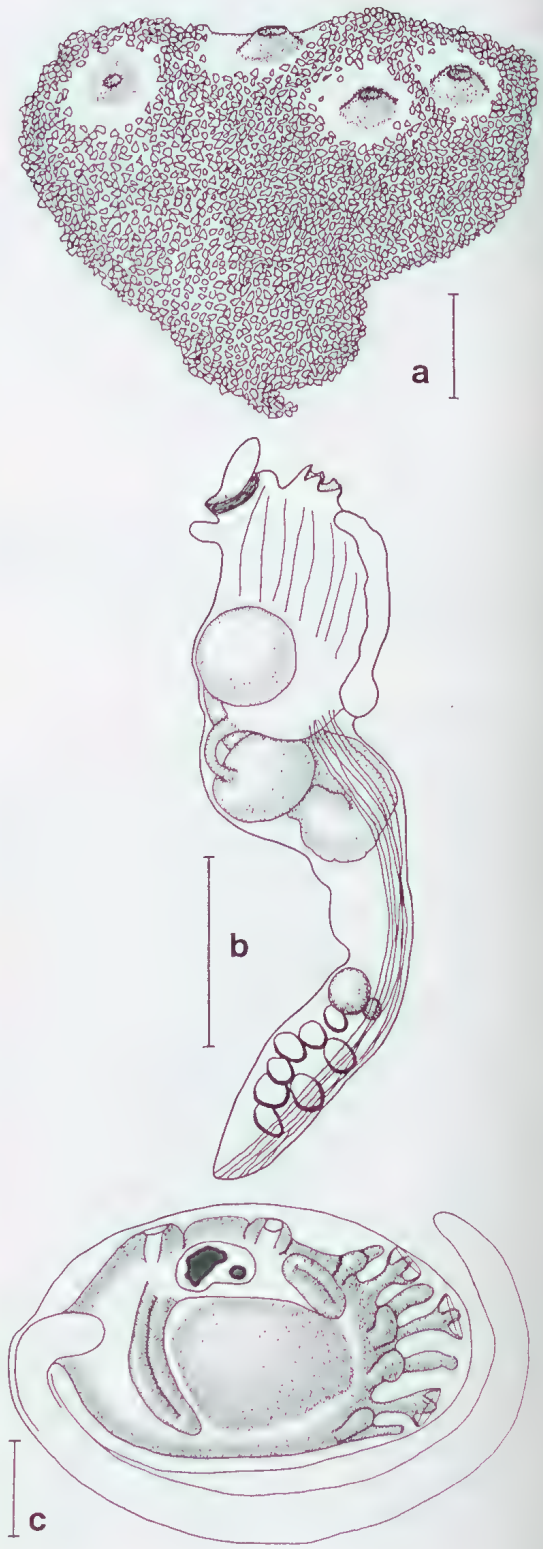


FIG. 48: *Synoicum durum* n.sp. (holotype QM U3990) — **a**, colony; **b**, zooid; **c**, larva. Scales: **a**, 2mm; **b**, 0.5mm; **c**, 0.1mm.

there are 6 distinct lobes. The rounded atrial lip is produced from the upper rim of the atrial siphon. A distinct median dorsal papilla is behind the atrial siphon. There are about 10 rows of 15 stigmata. The oesophagus curves ventrally to enter the large, smooth walled stomach. A gonad-free part of the posterior abdomen is behind the abdomen, but the posterior two-thirds of the abdomen is occupied by the irregular double row of large male follicles with the small ovary anterior to them.

Up to 2 embryos are in the posterior half of the atrial cavity. Tailed larvae are amongst the smaller viviparous larvae known, having a trunk only about 0.4mm long. They have median and lateral ampullae, and an otolith and ocellus. The tail is wound about three quarters of the way around the trunk.

REMARKS

These colonies do slightly resemble those of the New Zealand *S. kuranui* Brewin, 1950 which, however, has shallow circular swellings on the stomach wall, giving it a slightly mulberry-like appearance. The species also resembles *S. suarenum* n. sp., having an atrial lip from the upper border of the opening, a smooth stomach, a dorsal papilla, embryos being incubated in the posterior half of the atrial cavity, and circular systems opening on the flat upper surface of the colony lobes. There is, however, a difference in the relative size of the zooids and larvae in these two species, viz. 2mm and 0.4mm respectively in *S. durum*, and up to 1cm and 0.6mm in *S. suarenum* n. sp.

Synoicum erectum n. sp.
(Fig. 49)

DISTRIBUTION

TYPE LOCALITY: Victoria (south of Warnambool, 250 – 350m, from shark lines, coll. V. Johnstone 14.5.69, holotype MV F59367). South Australia (SSW Eucla 33°17'S 128°12'E, 18m, CSIRO RV *Soela* 13.1.89, paratype SAM E2554).

FURTHER RECORD: Victoria (27mls east of Gabo I., SAM E2555).

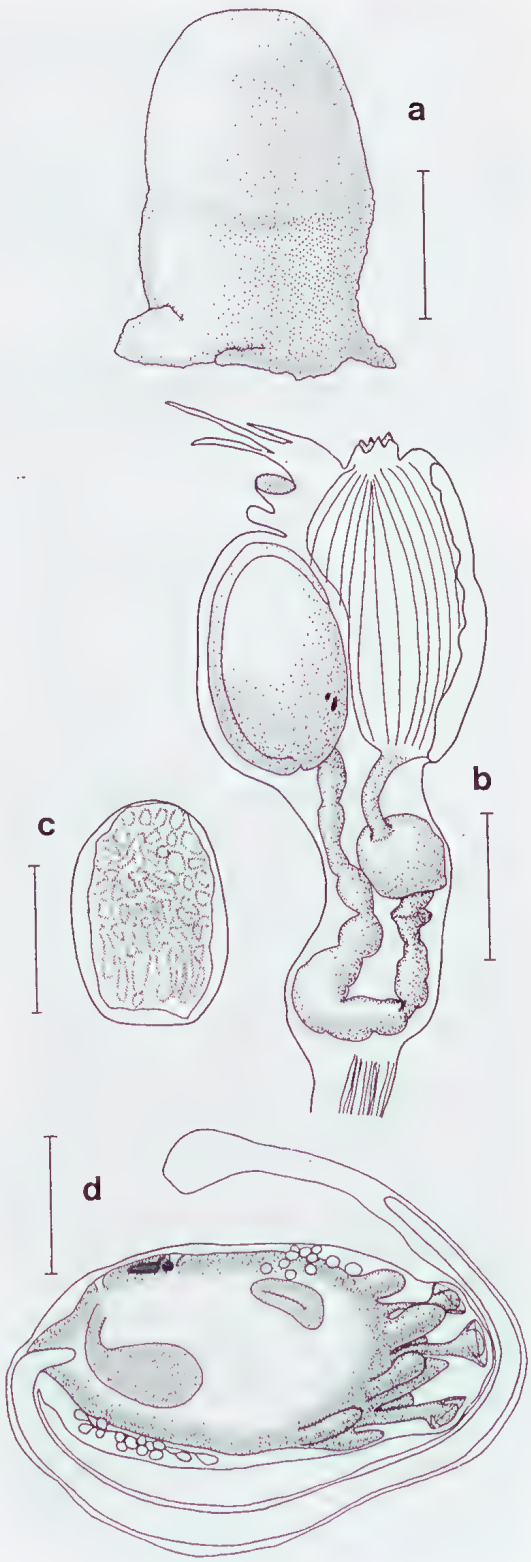


FIG. 49: *Synoicum erectum* n.sp. — **a**, colony outline (paratype SAM E2554); **b**, thorax and abdomen with embryo in atrial cavity (holotype MV F59367); **c**, internal wall of stomach (paratype SAM E2555); **d**, larva (holotype MV F59367). Scales: **a**, 1cm; **b**, **c**, 0.5mm; **d**, 0.2mm.

DESCRIPTION

EXTERNAL APPEARANCE: The holotype colony has been mutilated, but it appears to have been an upright cone, 3cm high and about 3cm in diameter across the flat base. The colony is covered with a thin layer of sand. Some root-like processes spread out around the base. Internally the test is very soft with only sparse embedded sand grains. Zooids, opening to the surface around the upper part of the cone, are crowded, possibly in circular systems. There is no trace of pigmentation in these zooids.

The Gabo I. and the paratype colonies are very similar to one another, smaller (to 2.5cm high) than the holotype, and retaining red colour in the zooids which are seen through the relatively light encrustation of sand on the upper half of the colony. The lower half of each of these colonies is slightly reduced in diameter and is more thickly encrusted with sand, forming a short, thick stalk. The base of the stalk is packed with embedded sand, but there is very little sand embedded in the rest of the soft internal test. Crowded circular systems of 8 to 9 zooids can be seen around the top half of each colony.

INTERNAL STRUCTURE: Zooids are robust, but when contracted the thorax and abdomen are less than 1mm long. The posterior abdomen is long. Branchial lobes are well defined, but relatively shallow. The atrial lip extends out from the anterior border of the aperture, long and fleshy, sometimes bifid at the tip, sometimes undivided and pointed, or with a fringe of up to 10 points on the straight edged tip. There is a small median dorsal papilla behind the atrial aperture. Longitudinal muscles (about 12) from the thorax extend back along each side of the zooid to its posterior extremity.

The pharynx has about 12 rows of about 8 stigmata, but these were difficult to count, as all the colonies have contracted zooids. The gut loop is almost the same length as the thorax in most of the examined zooids, but, as the thoraces are invariably more contracted than the abdomen, this ratio probably varies with the condition of the zooids.

The oesophagus is long, narrow and curves to enter the stomach. The stomach wall usually has glandular thickenings of the inner wall. However sometimes (SAM E2555) there are mulberry-like external swellings on some parts of the stomach. The distal part of the descending limb of the gut loop has the usual long duodenum, expanded mid-intestine, posterior stomach, and narrow intestine opening into the rectum at the proximal end of the ascending limb of the loop. The posterior abdomen is long and cylindrical. Only the ovary could be clearly identified, halfway down the posterior abdomen of the Gabo I. specimen (MV F2555).

Up to 2 embryos are incubated in the atrial cavity of specimens collected in May (MV F59637) and October (SAM E2555). They were not present in the paratype colony collected in January (SAM E5554). The larval trunk is about 0.7mm long, and the tail is wound about three quarters of the way around it. There are median and lateral ampullae, and patches of postero-ventral and antero-dorsal epidermal vesicles.

REMARKS

The zooids are small (though not as small as those of *S. prunum*), but the larval trunk is longer than usual for *Synoicum* spp. *Synoicum sacculum* n. sp. has a similar temperate range to the present species; and it also has the atrial lip from the upper rim of the aperture, a mulberry-like stomach, narrow thoraces, and red zooids and colonies. However, *S. sacculum* n. sp. has a short posterior abdomen with bunched male follicles, a brood pouch constricted off from the thorax, and larvae with a shorter trunk than those of the present species. Also, *S. sacculum* has a multilobed colony with a naked surface that is produced into rounded protrusions over each system of zooids (unlike the present species which has a fine encrustation of sand and a smooth external surface).

The sandy lobes of this species resemble those of *S. partitionis* Monniot, 1987, from New Caledonia. The latter species is distinguished by its wide pharynx with 18 rows of stigmata as well as by its tropical occurrence.

Synoicum galei n. sp.

Macroclinum hypurgon: Michaelsen, 1930, p.535 f. galei.

Not *Synoicum hypurgon*: Kott, 1963, p.86 (> *Aplidium* spp.); 1976, p.62 (< *Polyclinum fungosum*).

DISTRIBUTION

TYPE LOCALITY: Western Australia (Fremantle — Michaelsen 1930).

FUTHER RECORDS: None.

DESCRIPTION (after Michaelsen 1930)

EXTERNAL APPEARANCE: The colonies are irregular, flat topped cushions or sheets, with broad ridges and furrows on the surface, up to 5cm in maximum dimension and 1.8cm high. The test is

soft, but with a tough, thin outer cuticle. Zooids (from 4 to 11) are arranged in circular to oval systems. The cloacal apertures are sessile, and depressed into a groove. Sparse sand is present on the margin, but the upper surface of the colony is naked.

INTERNAL STRUCTURE: The zooids are about 1cm long, of which about 8mm is posterior abdomen. The thorax is longer than the abdomen. The branchial lobes are inconspicuous. The atrial siphon has the tongue extending from the upper rim of the aperture. Two loose bands of muscle extend along each side of the zooid to its posterior end. The stomach is smooth-walled. A brood pouch is constricted off from the postero-dorsal corner of the thorax. It always contains 2 embryos.

REMARKS

Despite the difference in colonies and the absence of the faecal pellets that occur in the type specimen from New Zealand, Michaelsen (1930) assigned the Western Australian specimen to *S. hypurgon* on the basis of the similarities in the zooids. However there are differences between the New Zealand and Fremantle colonies, and they are not conspecific. A new species is erected to accommodate the Fremantle specimens referred to *S. hypurgon* f. galei: Michaelsen, 1930. The species is distinguished from others which have the atrial lip associated directly with the rim of the aperture by the smooth stomach wall, absence of a dorsal papilla, and the flat-topped irregular colony with surface ridges and furrows.

Kott (1963), interpreting the dark oval bodies embedded in the test as faecal pellets, assigned colonies — one each from Heron I. and Rottnest I. — to the present species. Re-examination of these specimens (AM Y1382 U3991) has shown them to be *Aplidium lobatum*.

Embryos are incubated in a brood pouch (as they do in the present species) in *S. sacculum* n. sp., which has lobed colonies, a dorsal papilla and a mulberry-like stomach wall distinguishing it.

The broad ridges and furrows on the surface are reminiscent of those in *Aplidium crateriferum* and *A. lobatum* n. sp. However the latter species has a distinctive zooids which more closely resemble those of *S. papilliferum* (see below) than of the present species.

Synoicum intercedens (Sluiter, 1909) (Fig. 50)

Morchellium intercedens Sluiter, 1909, p.108.

Synoicum intercedens: Monniot and Monniot, 1987, p.81.

?*Synoicum suesanum* Michaelsen, 1919, p.27.

DISTRIBUTION

NEW RECORDS: Queensland (Capricorn Group, QM GH5084–5101 GH5105–7 GH5180 GH5182 GH5193 GH5253 GH5256 GH5282 GH5499 GH5566 GH5571–2 GH5591–2 GH5608 GH5672).

PREVIOUSLY RECORDED: Indonesia (Sluiter 1909). Moorea, Tahiti (Monniot and Monniot 1987).

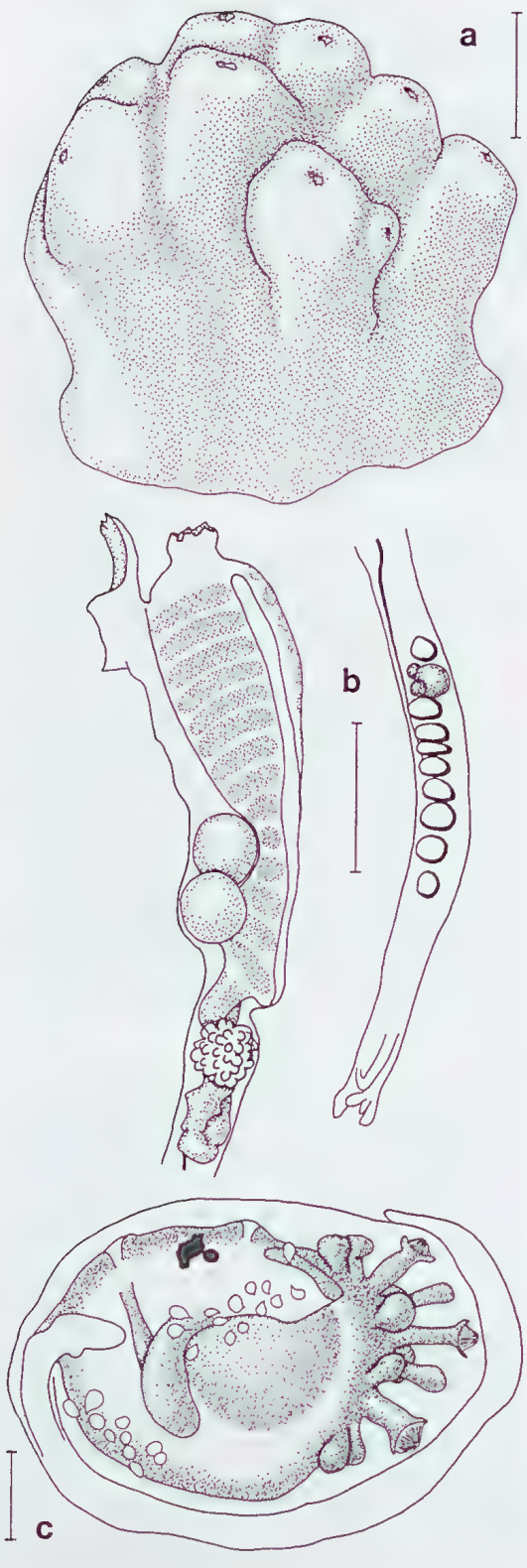
Although at present there are no records from Australian locations, other than those from the southern end of the Great Barrier Reef, it is probable that the species will be found generally around the northern part of the continent and in the western Pacific.

DESCRIPTION

EXTERNAL APPEARANCE: The colonies form cushions up to 3cm long with the upper surface divided into low, rounded swellings to domes from 3 to 10mm in diameter, projecting up to 5mm from the solid sandy basal common test and outer margin of the colony. Each of these protuberances has a large central sessile common cloacal aperture. One specimen has a few randomly distributed test swellings each containing a single system of juvenile zooids on the surface of a mass of firm gelatinous basal test (QM GH5090) and probably is a regenerating colony. Sometimes only a shallow crease is in the surface test delineating the circular area that is homologous with a rounded projection in other specimens. Sand sometimes lies in the crease between the surface swellings, and is present in the basal test. Up to 10 zooids are in each system.

The test is particularly opaque and firm in consistency in larger colonies, but is transparent and soft but firm in small ones. The living colonies are a chestnut or claret colour, or 'claret brown', or 'chocolate brown', or 'aster purple' (Ridgeway 1886), with 'madder brown' cells throughout the test. Some small colonies, when living, are described as 'red cherries projecting from sandy base and margin'. Zooids are 'burnt carmine' or 'aster purple' (Ridgeway 1886), or brownish-black. Basally colonies are yellowish, probably owing to the embedded sand showing through the brown test. In preservative the colonies are light yellowish, cloudy and translucent and the zooids are reddish-brown.

INTERNAL STRUCTURE: Zooids are up to 1cm long. Six rounded lobes surround the branchial aperture. The atrial siphon is relatively large, its



upper border is produced into a long lip with 3 small lobes on its tip. Sometimes the atrial lip curves around to form a tube with its lumen continuous with that of the siphon itself. A small papilla projects from the dorso-median line near the base of the posterior border of the atrial siphon. Eight fine longitudinal and oblique muscles are on the thorax and these extend along each side of the abdomen and posterior abdomen in a narrow band. There are 14 to 17 rows of 12 to 14 stigmata. The oesophagus is curved, entering the relatively short dorsal border of the stomach. The stomach wall is covered with rounded prominences (mulberry-like). The duodenal area is wide, the mid-intestine inflated and an oval posterior stomach is in the bend of the gut loop. The anal opening is about one-third of the distance up the thorax.

Gonads are in the middle third of the posterior abdomen, the small ovary behind the most anterior of the testis follicles, which extend back in a single series, or are bunched together when muscles contact.

Two embryos (but not tailed larvae) are in the posterior part of the atrial cavity of specimens collected in November (QM GH5087). Specimens collected in April and May have 3 embryos including a tailed larvae lined up in the atrial cavity (QM GH5088 GH5091). The larval trunk is about 0.50mm long. It has median and lateral ampullae alternating with the adhesive organs. Epidermal vesicles branch off strands that extend along each side of the mid-dorsal line as in *Polyclinum*, but ventral vesicles appear to be median. The lateral ampullae sometimes appear to have lost their connection with the epidermis.

REMARKS

The species is distinguished from others by its surface swellings each containing a circular system, and its mulberry-like stomach. The surface swellings are very variable and they are not always conspicuous. Thus the fact that Sluiter (1909) did not observe them may not be significant. Other characters of the newly recorded material conform with the type specimen, and the Australian and Indonesian specimens appear to be conspecific. *Synoicum intercedens*: Monniot and Monniot, 1987, has fewer rows of stigmata than either the type or the present Australian specimens, and the number of stigmata per row

FIG. 50: *Synoicum intercedens* — **a**, colony (QM GH5087); **b**, zooid (QM GH5087); **c**, larva (QM GH5107). Scales: **a**, 5mm; **b**, 1mm; **c**, 0.1mm.

has not been reported. Otherwise these French Polynesian specimens appear to conform with the type material. *Synoicum suesanum* Michaelsen, 1919 has similar colonies with circular systems, and 13 to 15 rows of stigmata with 10 to 12 per row. Michaelsen (1919) distinguished the species by the depression separating the systems. However that depression sometimes occurs in *S. intercedens*. There is no known character separating *S. suesanum* from the present one.

The new Australian temperate species *Synoicum sacculum* n. sp. has a mulberry-like stomach, but its systems are not separated from one another by grooves or depressions, and a single embryo is incubated in a stalked brood pouch. The tropical *Synoicum suarenum* n. sp. which is sympatric with *S. intercedens* and is the same dark colour has, like *S. sacculum* n.sp., many circular systems in each of its wedge-shaped lobes, and lacks grooves or subdivisions which, in the present species, tend to isolate the systems from one another. *Synoicium suarenum* n.sp. is further distinguished by its smooth-walled stomach and larger larval trunk.

Synoicum macroglossum (Hartmeyer, 1919) and *S. tropicum* (Sluiter, 1909) are also distinguished from the present species by their smooth-walled stomachs.

Synoicum longistriatum n.sp.
(Fig. 51)

DISTRIBUTION

TYPE LOCALITY: Western Australia (off Cockburn Sound, 32°S 155°08'E CSIRO Cruise 144/DM4/63, 110m, coll. L. Thomas 28.8.63, holotype QM GH5583.

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: The colony is an upright, almost cylindrical lobe, slightly expanded terminally. It is 7cm high and about 3cm in diameter. Basally there are sandy root-like projections of the test. The lower third of the lobe, comprising the lower part of the stalk, is transversely wrinkled, and covered with a layer of sand. The middle third has a layer of finer sand and is not wrinkled. The naked upper third has openings of the crowded zooids. These, seen through the transparent test, appear to be arranged in crowded longitudinal rows converging to cloacal apertures on the terminal free end. The crowded zooids are perpendicular at the surface, but posteriorly they curve down into the stalk of the colony.

INTERNAL STRUCTURE: In this colony a large quantity of sand fills the pharynx of most of the zooids, obscuring its structure. The branchial apertures have 6 lobes, and atrial apertures are large openings with the upper rim extended out to form a tongue. About 12 fine longitudinal muscles are in the thoracic body wall. These extend along the length of the abdomen and posterior abdomen. Stigmata are in 16 rows of about 16. The stomach is large and voluminous, without longitudinal folds, but sometimes collapsing into irregular or horizontal ones. Double rows of male follicles are in part of the long posterior abdomen of some of the zooids, although the ovary was not detected.

FIG. 51: *Synoicum longistriatum* n.sp. (holotype QM GH5583) — colony. Scale: 1cm.

REMARKS

The colony is distinctive and unique in this genus, superficially resembling that of *Distaplia australiensis* (see Kott 1990). However, the zooids are characteristic of the Polyclinidae. The *Aplidium* species with longitudinal double-row systems converging to the top of the head, viz. *A. australiense*, *A. geminatum* n.sp., *A. inflorescens* n.sp. and *A. paralineatum* n.sp. are distinguished by their numerous stomach folds. The shape of the colony and its sandy surface resembles *S. atopogaster*, but the form of the systems differ.

It is unfortunate that this unique specimen is not well preserved. Nevertheless as it is a unique colony form and unlikely to be confused with other species in this genus, it is considered appropriate for it to be designated holotype. It is probable that damage was caused to the specimen by the way it was collected (beam trawl), rather than its treatment after collection.

Synoicum macroglossum (Hartmeyer, 1919)
(Fig. 52. Plate 9a)

Macroclinum macroglossum Hartmeyer, 1919, p.126.

DISTRIBUTION

NEW RECORDS: Queensland (Heron I., QM GH5055; Mackay, QM GH5421).

PREVIOUSLY RECORDED: Western Australia (Cape Jaubert — Hartmeyer 1919).

DESCRIPTION

EXTERNAL APPEARANCE: One colony (QM GH5055) is a large flat-topped cushion 6cm in diameter, 2cm high, with rounded margins and a vertical border. Sand is present on the base and around the border, but not on the upper surface. Sparse sand is present internally in the lower half of the colony, but it becomes even more sparse toward the centre, as if it was gradually moving in from the sandy outer border. The colony from

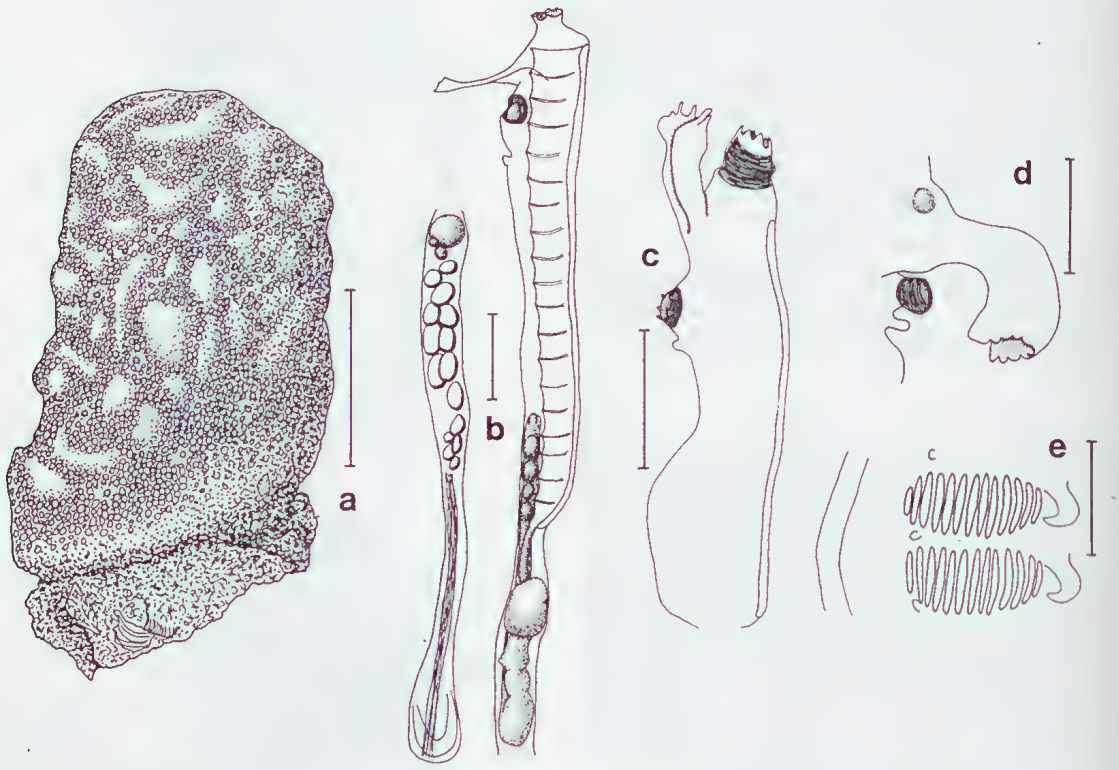


FIG. 52: *Synoicum macroglossum* — **a**, colony (QM GH5421); **b**, whole zooid severed between thorax and posterior abdomen (QM GH5055); **c**, **d**, thorax and atrial aperture, with atrial lip shown in different positions (QM GH5421 GH5055); **e**, portion of right branchial wall (QM GH5055). Scales: **a**, 2cm; **b**, **c**, 1mm; **d**, **e**, 0.5mm.

Mackay is an upright cone, 6cm high, with sand around the base and sparsely embedded through the test.

The test is translucent and gelatinous but firm and rigid in both specimens. Circular to long, low swellings, with shallow depressions between them are on the upper surface. The small and inconspicuous branchial openings can be seen around the periphery of the swellings, and in the depressions between them. Large cloacal apertures occur in the depressions, especially where 2 or more converge. These apertures either are sessile, or they protrude on surface swellings created by thickened test over the circular cloacal cavities that are formed at the junctions of the cloacal canals.

Internally the posterior ends of the zooids crisscross one another. The test is pale yellowish-brown to greenish-yellow in preservative, and the preservative itself is stained yellow-orange. One living specimen (QM GH5055) was, 'mummy brown' internally and 'seal brown' (Ridgeway 1886) on the surface. The other (from Mackay) is said to have been black when living.

INTERNAL STRUCTURE: Zooids are long (to 1.5cm) and narrow. The thorax is about one-third of the length of the zooid, and the abdomen and about half of the gonad bearing part of the posterior abdomen together comprise another third. Eight longitudinal muscles extend the length of the thorax, and are reduced to 2 or 3 each side of the abdomen and posterior abdomen. The branchial aperture is on a trumpet-shaped siphon that appears to be fixed in the firm surface layer of test. A sphincter is around the base of the siphon. The long, muscular atrial lip has a dentate tip, and is difficult to remove from the test where it lies over the top of the cloacal cavity. It arises from the body wall opposite the first row of stigmata, anterior to the muscular atrial aperture which lies opposite the third row of stigmata. A sphincter is also present around the atrial aperture. When contracted, the atrial lip curves over the aperture. A papilla projects from the body wall just behind the atrial siphon opposite the fifth row of stigmata. Nineteen rows of 12 to 14 fairly long stigmata are in the branchial sac, although the number reduces posteriorly. A wide strip of unperforated test is each side of the endostyle. There is a minute papilla on each transverse vessel at about the level of the third ventral stigma on each side of the body. A row of robust dorsal languets are to the left of the dorsal mid-line.

The gut loop is vertical and narrow — the oesophagus curves ventrally to enter the bilaterally symmetrical, smooth-walled stomach. The duodenum is large, the mid-intestine inflated and a large oval posterior stomach is in the bend of the gut loop. The bilabiate anus opens at the level of the fourth row of stigmata from the posterior end of the thorax.

A very short gonad-free part of the posterior abdomen is behind the gut loop. A small ovary is anterior to the oval testis follicles which are in 2 longitudinal series, alternating with one another. Sometimes (but not always) an extent of the posterior end of the posterior abdomen is free of gonads. A V-shaped heart is in the posterior extremity of the posterior abdomen. The newly recorded specimens collected in November, have well-developed ovaries, but no embryos were found.

REMARKS

The species is distinguished by its protruding atrial siphon, separate atrial lip, narrow zooid and robust cushion-shaped colony. The type specimen differs from the present one in the presence of a layer of sand on the upper surfaces as well as around the margin; and in the presence of up to 14 rows of stigmata rather than the 18 of the present eastern Australian colonies. Hartmeyer (1919) did not observe the small branchial papilla toward the ventral end of each transverse vessel, but these are inconspicuous and obscured unless the thorax is completely relaxed.

The dorsal papilla and separate atrial lip are like *S. papilliferum* (Michaelsen, 1930) and the zooids also have similar numbers of stigmata. However, although Michaelsen believed the dorsal papilla was unique to his species (see below), it occurs in both *Polyclinum* and *Synoicum*. Although the conspicuous cloacal apertures and long curving double row systems of the present tropical species may be different from *S. papilliferum* (in which Michaelsen did not find any cloacal apertures and could not determine the form of the systems), at present the only character definitely known to separate the species is the presence of sand adhering to the external test of the temperate *S. papilliferum*. Species of *Aplidium* with similar zooids (e.g. *A. lobatum*, *A. cratiferum*) lack a median dorsal papilla, and have different systems from those of the present species. *Synoicum chrysanthemum* has similar systems, but the colonies are different.

Synoicum obscurum n.sp.
(Fig. 53)

DISTRIBUTION

TYPE LOCALITY: Victoria (Bass Strait, reef off Ninety-mile Beach, 90km SW of Lakes Entrance, coll. J. Watson R3E/36 1977, holotype QM G12726, paratype QM G12727).

FURTHER RECORD: NSW (Arrawarra, QM GH5589).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are thick mats with sand crowded throughout making them hard and brittle. The mats are made up of sandy cone-shaped, upright lobes which adhere closely to one another. The terminal free ends of these lobes project from the upper surface of the colony as rounded swellings, each of which accommodates a circular system of up to 12 zooids. Zooids are tightly enclosed in the sand and hard to remove from it although the thin channels that accommodate the zooids are rigid. The zooids surround a shallow common cloacal cavity (in the terminal end of each lobe) which opens through a common cloacal aperture in the centre. Branchial apertures are inside, and protected by, the rounded margin of the terminal end of each lobe. The cloacal cavities beneath the upper surface of colony confer a loose appearance to the surface layer of brittle sand-filled test.

INTERNAL STRUCTURE: The zooids are relatively muscular, with about 20 longitudinal bands on the thorax. These muscles extend posteriorly to form a band along each side of the mid-ventral line. Zooids are relatively long, even when contracted the thorax, abdomen and gonad-bearing anterior part of the posterior abdomen are about 6mm long, while the long posterior part of the posterior abdomen, without gonads in it, extends into the sandy base of the colony.

The 6 branchial lobes are rounded. An atrial siphon protrudes from the dorsal surface, and a flat atrial tongue with a tridentate tip is produced out from the upper rim of the opening. The lower rim of the atrial opening is divided into 3 small lobes. A pointed median dorsal papilla is at the base of the atrial siphon. About 20 rows of up to 20 stigmata appear to be present, although the pharynx is too contracted for accurate counts. Irregular internal glandular areolations of the stomach wall are present, especially on the mesial side of the stomach (against the intestine). A few

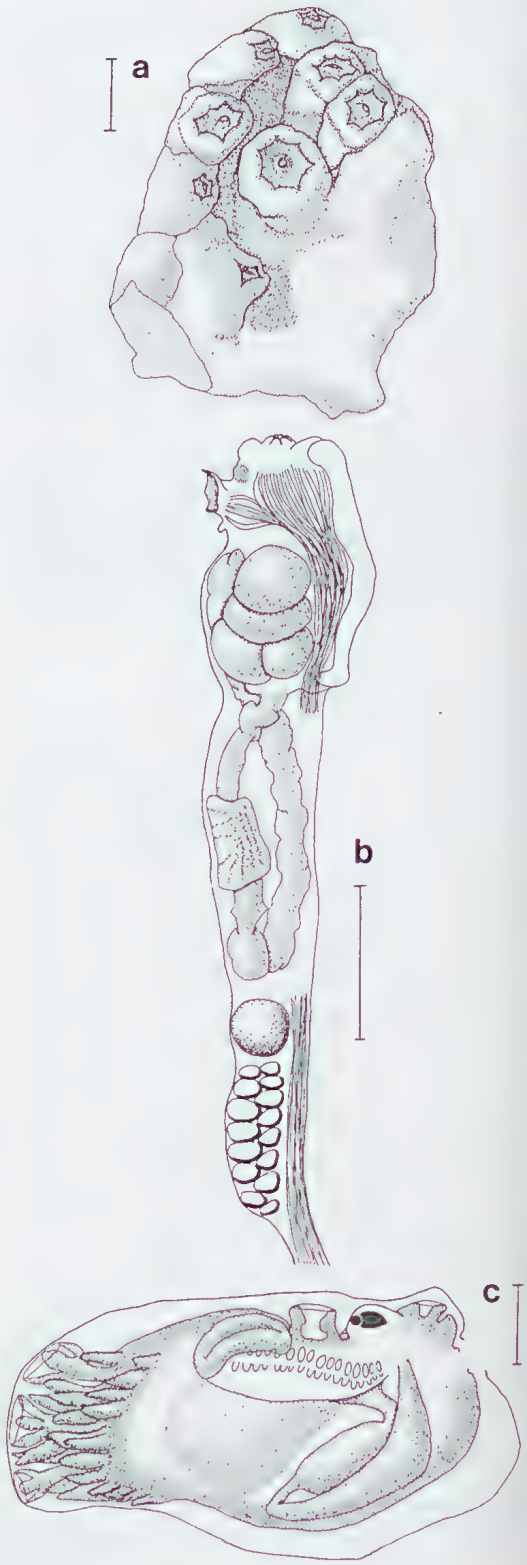


FIG. 53: *Synoicum obscurum* n.sp. (holotype QM G12726) — **a**, colony; **b**, zooid; **c**, larva, tail removed. Scales: **a**, 5mm; **b**, 1mm; **c**, 0.1mm.

of these shallow glandular areas sometimes form irregular longitudinal ridges which resemble the longitudinal folds of *Aplidium*. The duodenal, mid-intestinal and posterior stomach regions are characteristic for the genus.

In the type material, a large ovum is present behind the gut loop, anterior to a short double longitudinal series (about 8 per series) of testis follicles. The posterior abdomen continues posterior to the testis follicles, which protrude dorsally from it as a result of the contraction of the ventral muscles. Four or 5 embryos are crowded in the atrial cavity.

The larval trunk is 0.6mm long. The anterior end is obscured by numerous narrow ectodermal ampullae. There are 3 median adhesive organs, and an ocellus and otolith are in the cerebral vesicle.

REMARKS

A similar colony form is found in many species of *Aplidium* (e.g. *A. bacculum* n.sp., *A. filiforme* n.sp.). However, despite the presence of some longitudinal glandular ridges in the stomach wall, the present species is distinguished from the genus *Aplidium* by the shape of its zooids with a relatively primitive lobed atrial opening and the median dorsal papilla.

Synoicum durum has colonies consisting of sandy lobes, but the test above each system is naked, and each lobe has 2 or 3 systems.

Synoicum papilliferum (Michaelsen, 1930)

Macroclinum papilliferum Michaelsen, 1930, p.530.
Synoicum papilliferum: Millar, 1966, p.360. **Not** Kott, 1963, p.87 (< *Polyclinum tenuatum* n. sp.); 1972a, p.16; 1972b, p.177 (< *S. sacculum* n. sp.).

DISTRIBUTION

NEW RECORDS: None.

PREVIOUSLY RECORDED: Western Australia (Bunbury — Michaelsen 1930). Victoria (Nepean Peninsula — Millar 1966).

DESCRIPTION (after Michaelsen 1930)

EXTERNAL APPEARANCE: Colonies are cushion shaped or irregular sheets, up to 3cm diameter and 2.4cm high. Sometimes they are fixed by a narrowed base. The preserved colonies are transparent and yellowish, with an external layer of sand. Some sand is present internally but it is not as crowded as it is externally. The outer layer of test is tough. Cloacal cavities are present at the level of the atrial apertures, but cloacal apertures were not seen.

INTERNAL STRUCTURE: The zooids are vertically arranged in the test, with their posterior abdomina criss-crossing. The body wall is delicate with about 10 longitudinal muscle bands. The branchial siphon is conspicuous with a well developed sphincter at its base. The short atrial siphon, surrounded by a sphincter muscle, projects laterally from the body wall a short distance behind the atrial lip, which is narrow, but not long, and its tip is produced into 2 or 3 small papillae. A conspicuous median papilla projects from the body wall just behind the atrial siphon. Sixteen or 17 rows of 9 or 10 stigmata are in the long, narrow thorax. The oesophagus curves to enter the smooth stomach which is about halfway down the abdomen. A short gonad-free area is behind the abdomen, in front of the single row of male follicles that occupies the rest of the narrow posterior abdomen. When the posterior abdomen contracts, the male follicles are drawn up into a double row. Two short vascular stolons project from the end of the zooid.

REMARKS

Although Michaelsen thought the papilla was unique, it does occur in species of *Polyclinum* as well as in other *Synoicum* species. Nevertheless Kott (1963; 1972a,b) followed Michaelsen and assigned specimens of *S. sacculum* n. sp. and *Polyclinum tenuatum* to this species because, like *S. intercedens* and *S. suarenum* n.sp., they had a dorsal papilla. However, all these species are readily distinguished from the present one by having the atrial lip extending from the anterior rim of the aperture. *Synoicum macroglossum* has both a separate atrial lip and a dorsal papilla, but is distinguished from the present species by its conspicuous cloacal systems with raised cloacal apertures and the absence of an external layer of sand.

Although they differ in having a dorsal papilla, zooids of the present species, with their long, narrow thorax, long muscular branchial siphon, and atrial siphon separate from the atrial lip, resemble those of certain *Aplidium* spp. (e.g. *A. cratiferum*, *A. lobatum*, see below). The stomach folds of some of these *Aplidium* spp. are few and indistinct, but they all have distinct cloacal systems that distinguish them from the present species.

Millar (1966) records that his specimens of *S. papilliferum* had all the features of the type specimens, except the dorsal papilla. However, as there

is no other known temperate species of *Synoicum* with similar characters, it is possible that the papilla was obscured in the material he examined.

Synoicum prunum (Herdman, 1899)
(Fig. 54. Plate 9b)

Psammaplidium prunum Herdman, 1899, p.84.
Synoicum prunum: Kott, 1963, p.87.

DISTRIBUTION
NEW RECORDS: New South Wales (Arrawarra, QM GH5394). Queensland (Bribie I., QM G2102; off Cape Tribulation, QM GH799).
PREVIOUSLY RECORDED: New South Wales (Port Jackson — AM G2101 Herdman 1899).

DESCRIPTION
EXTERNAL APPEARANCE: Like the holotype, the colony from Cape Tribulation is upright, oval, converging to a narrow sandy base produced into sandy roots. It is about 7cm high and 4cm in diameter. The specimen from Bribie I. is massive (14cm long and 9cm maximum diameter), lumpy, oval and football-shaped overall, but with deep creases dividing it into lobes. It has no obvious point of fixation.

The internal test always is firm and gelatinous with long tough fibres in it. It is almost opaque in preservative, while the outside layer is tough and hard with occasional patches of sand embedded. The long thread-like zooids are found withdrawn from the surface and criss-cross one another through the internal test. Their arrangement is obscure and the form of the systems was not determined.

INTERNAL STRUCTURE: Both newly recorded colonies are in a vegetative stage, many developing buds being present. Adult zooids are thin and thread-like. The very long, thin posterior abdomen is up to 2cm, being many times the length of the rest of the zooid (only about 2mm long when contracted). The contracted thoraces (QM GH799) are slightly longer than the abdomen, and when extended (QM G2102) they are at least twice the length of the abdomen. About 12 fine longitudinal muscles are on the thorax and these extend the length of the zooid in a band on each side. A single fleshy atrial lip continuous with the anterior rim of the atrial aperture has a straight tip with a single, small, pointed, median tooth. The branchial lobes are only shallow. A small dorsal papilla arising from the body wall behind the atrial aperture can be seen in the contracted zooids, but was not detected in the extended ones.

Fourteen dorsal languets were counted in the specimen from Cape Tribulation, indicating that there are 15 rows of stigmata, the same number as in the Bribie I. zooids. The thoraces are characteristically narrow and up to 8 stigmata per row were counted. The abdomen is small. The narrow and characteristically long oesophagus curves to enter the smooth-walled, small stomach which is halfway down the abdomen. The relatively long duodenum, inflated mid-intestine and posterior

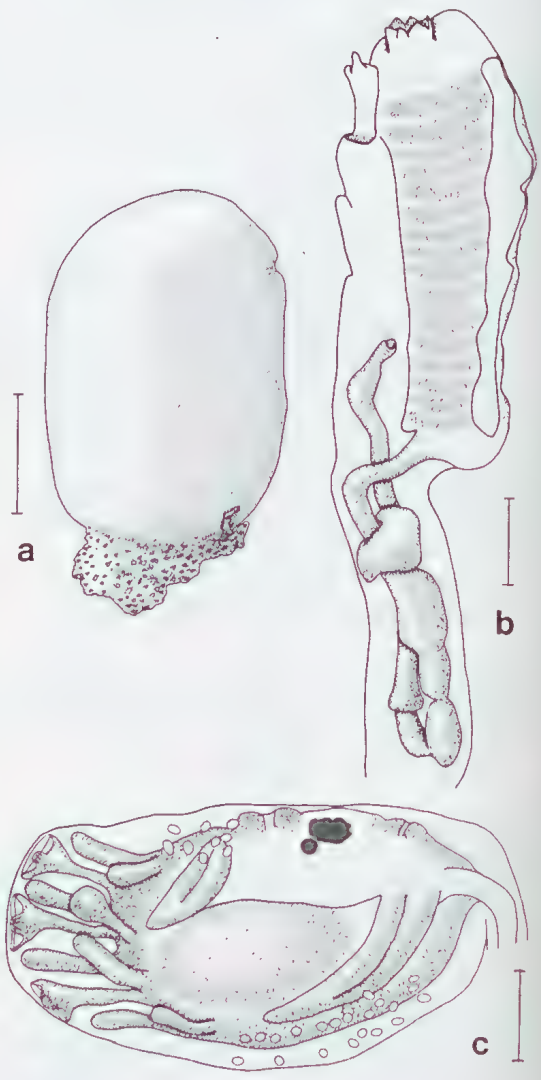


FIG. 54: *Synoicum prunum* — a, colony outline (QM GH799); b, thorax and abdomen (QM GH799); c, larva (holotype AM G2101). Scales: a, 2cm; b, 0.2mm; c, 0.1mm.

stomach are distal to the stomach in the descending limb of the gut loop. Gonads are not developed in the newly recorded specimens. They are present in the long posterior abdomen of the type specimen, which also has 2 embryos in the atrial cavity.

The larval trunk is 0.55 to 0.65mm long. It has median and lateral ectodermal ampullae alternating with the 3 median adhesive organs, and patches of ectodermal vesicles antero-dorsally and postero-ventrally.

REMARKS

The large, almost naked colonies of this species are unique in the Australian fauna. There are some dark, greenish-black colonies of *Polyclinum vasculosum* recorded from Moreton Bay that reach the same size as the present species and superficially can be confused with it. *Synoicum citrum* has naked but sessile colonies, smaller than those of *S. prunum*, with larger zooids, fewer rows of stigmata and more stigmata per row.

Synoicum sacculum n. sp.
(Fig. 55. Plate 9c–e)

Synoicum papilliferum: Kott 1972a, p.16; 1972b, p.177; 1976, p.62.

DISTRIBUTION

TYPE LOCALITY: South Australia (Waldegrave I. in caves, 2m strong waves, coll. S. Shepherd 25.11.73, holotype SAM E2556, paratypes QM GH5044). Victoria (Flinders, jetty piles, 5m, coll. N. Coleman 18.6.77 AMPI 201, paratype QM G10163).

FURTHER RECORDS: South Australia (St. Vincent Gulf, West I. — Kott 1972a; Thorny Passage, SAM E2491). Tasmania (W. Granville Harbour, SAM E2552).

The Tasmanian specimen was taken from a depth of 425m.

DESCRIPTION

EXTERNAL APPEARANCE: The colony consists of crowded sessile, flat-topped to rounded lobes about 1cm in diameter rising from a sandy basal membrane or test mass. Sometimes the lower half of the lobe is constricted to form a thick stalk with some sand embedded. Sand is sparse internally in the upper part of each lobe. Sand is sometimes present on the upper surface, although the test above the zooid systems is usually left naked. The test is very soft internally. Zooids form circular systems of 2 to 3mm diameter with up to 10 zooids around a central cloacal aperture. The cloacal apertures are about 2cm apart, and are evenly spaced on the top of each lobe. In one small (1.7cm high) flat-topped colony (SAM E2491) the branchial openings are around the outer margins of surface depressions, and sessile cloacal apertures are in the centre. The test is raised in firm rounded ridges between the depressions.

In life the lobes are bright red, with bright red zooids. In preservative the test is yellowish and translucent, and the preservative is stained a yellowish-red.

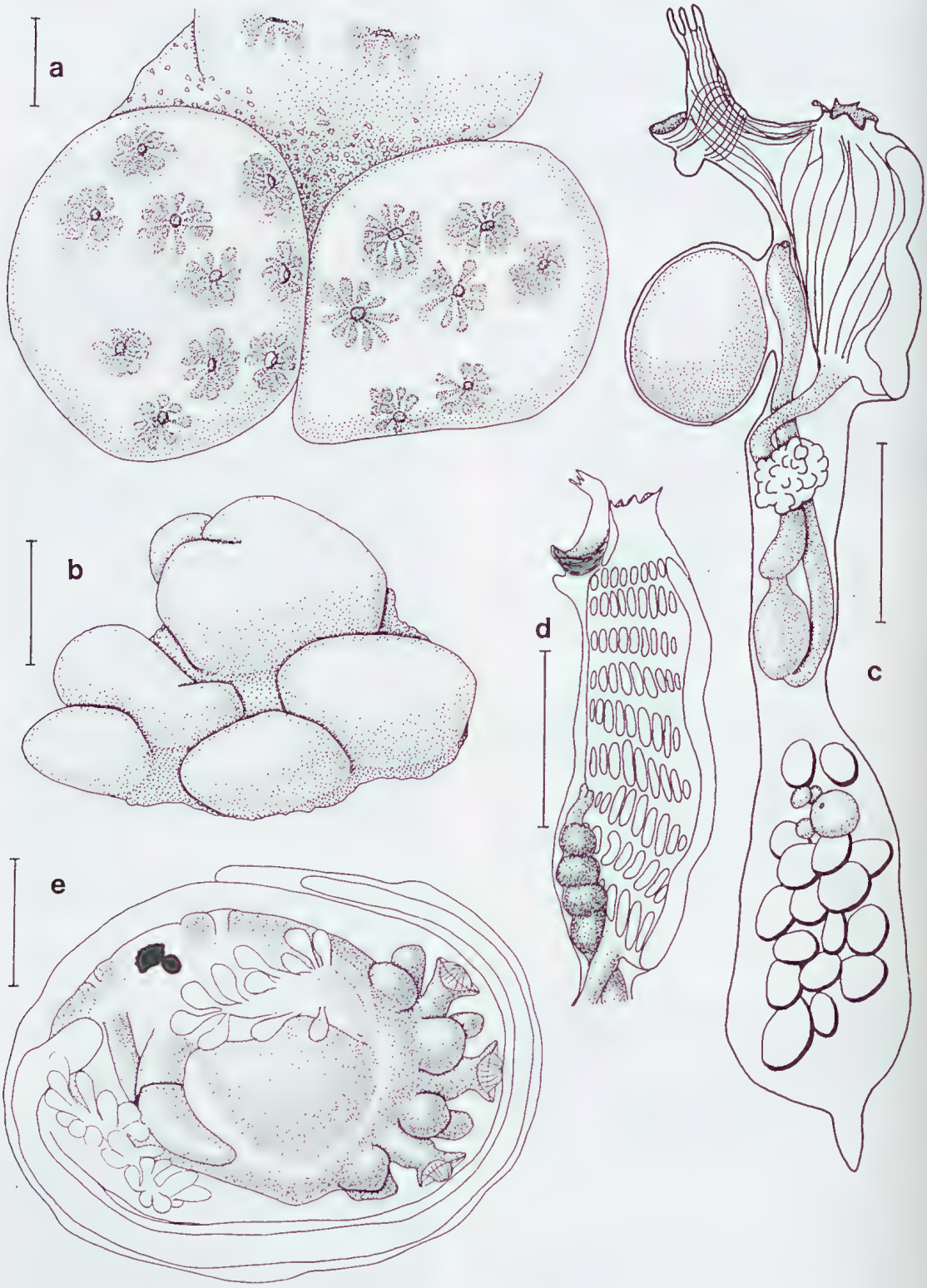
INTERNAL STRUCTURE: The zooids are 2 to 3mm long, with a short posterior abdomen. The thorax, abdomen and posterior abdomen are each about one third of the total length. There is a fine, short posterior vascular stolon. About 6 fine longitudinal and oblique muscles are on the thorax and these continue along the length of the zooid. Strong muscles extend from the branchial siphon along the atrial siphon (which often is long) onto the atrial lip which continues out from the anterior rim of the opening. The straight tip of the atrial lip has 3 narrow finger-like papillae evenly spaced along it. A papilla is in the mid-dorsal line behind the atrial aperture, sometimes carried out along the siphon when that is produced dorsally.

About 8 short stigmata are in 9 or 10 rows. The oesophagus is long and curved, and the stomach, about halfway down the abdomen has mulberry-like swellings in its wall. The duodenal area is long, the mid-intestine inflated, and an oval stomach is in the bend of the gut loop. The anal opening is opposite the third last row of stigmata. Colonies with large mature male follicles in the short posterior abdomen have about 20 bunched around the ovary (SAM E2491, QM GH5044). These colonies also have one to 3 embryos, up to the tailed larval stage, present in a brood pouch constricted off from the postero-dorsal corner of the thorax.

The larval trunk is almost spherical, 0.4mm in diameter, with otolith and ocellus, postero-ventral vesicles, and median and lateral ampullae anteriorly. The tail is wound about three quarters of the way around it.

REMARKS

The form and colour of the colonies is distinctive, as are the atrial lip from the anterior rim of the opening with finger-like papillae on its tip, the mulberry-like stomach, and the short posterior abdomen with bunched male follicles. The spherical larval trunk also is unusual. The brood pouch constricted off from the body wall is reminiscent of the one described for *Macroclinum*


a
b
c
d
e

hypurgon f. galei: Michaelsen, 1930 although the latter contains 2 embryos, its stomach is smooth, and its colonies are not lobed.

A dorsal papilla similar to the one in the present species, a short posterior abdomen and a similar atrial aperture occurs in the tropical species *S. suarenum* n. sp. However in the latter species the stomach is smooth, the larvae are not spherical and a brood pouch is not constricted off from the body wall.

Synoicum erectum, a species that overlaps the South Australian range of the present one, has sandy colonies consisting of single lobes rather than the many lobes of the present species. The zooids can be distinguished by their longer posterior abdomen, longer larval trunk and absence of a brood pouch.

Synoicum suarenum n. sp.
(Fig. 56. Plate 9f,g)

Synoicum kuranui: Kott, 1981, p.159.
Synoicum ?clavatum: Millar, 1975, p.255.

DISTRIBUTION

TYPE LOCALITY: Queensland (Capricorn Group, Wilson Reef, rubble zone, low tide, coll. P. Kott Jan 1977, holotype QM GH5080; Heron I., rubble zone, low tide, coll. P. Kott 4.11.86, paratype QM GH5070).

FURTHER RECORDS: Queensland (Capricorn Group, QM GH5066–9 GH5071–9 GH5081–3 GH5176 GH5178; Hardy Reef, QM GH5377; Lizard I., QM GH5277 GH5586); Fiji (Kott 1981). Indonesia (Millar 1975).

DESCRIPTION

EXTERNAL APPEARANCE: Flat-topped wedge- to top-shaped lobes, crowded together and narrowing to the base where they are joined by common basal test or by connecting strands to adjacent lobes. Sometimes the basal stalk portion of the lobe is branched and there are 2 heads from a basal common stalk. Colonies from Hardy Reef have long stalks (longer than those from Heron I.); narrowing toward the base. When alive and inflated the separate lobes that make up the colony appear confluent. The separate lobes are more apparent when it is removed from the substrate. The flat-topped lobes are up to 2.5cm high and up to 3.0cm in diameter at the top. In life colonies have a characteristic appearance resembling a pig's kidney both in colour and form. They are always opaque, shiny cherry coloured, crimson, and a dark maroon, plum colour, or 'pansy-' 'pomegranate-', 'Indian-' to 'aster-purple' (Ridgeway 1886). In preservative colonies become brownish-black, but the colour eventually is lost altogether. At first the preservative is stained orange-yellow, and clouds of brownish-black pigment cells are in the test. Circular cloacal systems of 4 to 8 zooids are evenly spaced over the surface. The central common cloacal apertures are in slight surface depressions about 2.5mm apart, and each system is about 2.5mm in diameter. The rim of each common cloacal aperture has small denticulations, into which the denticulations on the tip of the atrial lips of each zooid fit. The cloacal chambers are shallow and circular, being almost completely open to the exterior through the large cloacal aperture. The test is firm and gelatinous. Sand is absent from the surface, and from the internal test. Up to 15 systems occur in one lobe of the colony.

INTERNAL STRUCTURE: The zooids are less than 1cm in length, even when distended, and the thorax is half the total length of the zooid. The posterior abdomen is generally relatively short for a species of this genus. One or 2 short vascular appendages are at the posterior end of the posterior abdomen. The 6 branchial lobes are small and pointed. The atrial siphon is short but wide, with its upper border produced into a short, broad tongue with 3 to 5 short pointed teeth on its broad, straight outer edge. There is a median pointed papilla projecting out from the dorsal line behind the atrial aperture. About 12 fine longitudinal and oblique thoracic muscles in bands of moderate width extend along each side of the thorax and abdomen and are inserted into a projecting horn on each side of the posterior abdomen. Sixteen rows of 10 short, oval stigmata are in the branchial sac, each row reducing in length dorsally and ventrally. The oesophagus is curved and the dorsal border of the stomach between the oesophageal and duodenal openings is relatively short. The stomach wall is smooth externally, but internally it has some glandular areolations. The duodenal area is long, the mid-intestine inflated and an oval posterior stomach is in the bend of the gut loop. The bilabiate anus is about one-third of the distance up the thorax. The posterior abdomen is continuous with the abdomen and the gonads are in its posterior half, there being a narrow gonad-free neck of variable length behind the gut

FIG. 55: *Synoicum sacculum* n.sp. — **a**, **b**, colonies (paratype QM G10163, **a**, showing circular systems; **b**, colony outline); **c**, zooid with embryo in brood pouch (SAM E2491); **d**, thorax (paratype QM G10163); **e**, larva (paratype SAM E5044). Scales: **a**, 2mm; **b**, 1cm; **c**, **d**, 0.5mm; **e**, 0.1mm.

loop. The ovary is mixed in with the anterior testis follicles, which are either in one or 2 irregular longitudinal series or, when muscles are contracted, bunched in the posterior end of the posterior abdomen, giving it a sac-like appearance. There are about 20 testis follicles.

Embryos (up to 3) are in the posterior end of the atrial cavity of zooids collected in January, April and May. Tailed larvae have a trunk about 0.6mm long. Median and lateral ampullae are present. A postero-ventral cluster of epidermal vesicles is in the larval test each side of the mid-line, near the

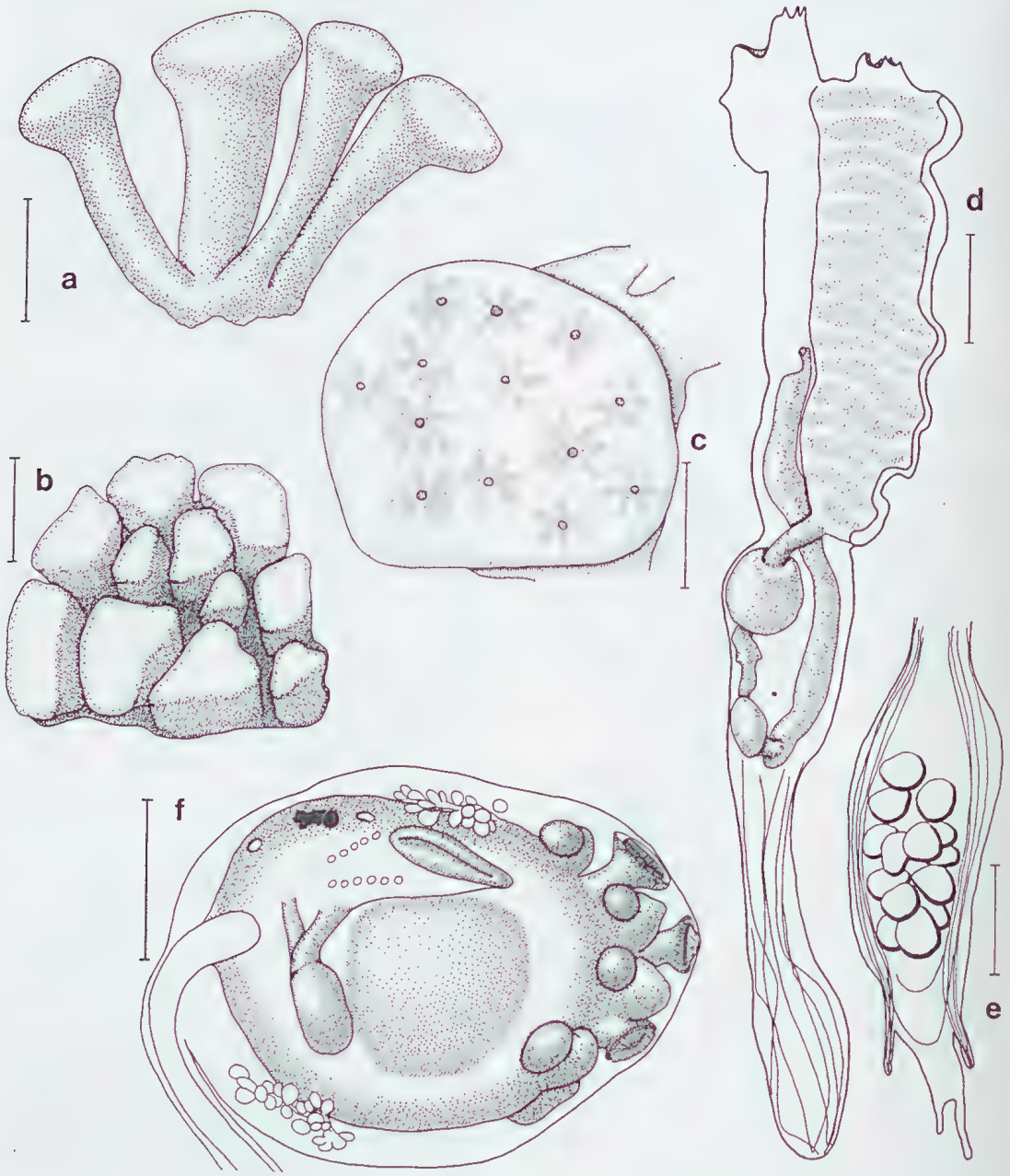


FIG. 56: *Synoicum suarenum* n.sp. — **a**, colony with longer lobes (QM GH5377); **b**, colony with short lobes (holotype QM GH5080); **c**, colony from above showing systems (QM GH5067); **d**, zooid (QM GH5067); **e**, posterior abdomen showing gonads bunched in posterior end (paratype QM GH5070); **f**, larva (QM GH5073). Scales: **a**, 1cm; **b**, 2cm; **c**, 5mm; **d**, **e**, 0.5mm; **f**, 0.2mm.

base of the tail. These separate from an epidermal strand that trails posteriorly through the test, from each side of the mid-line ventral to the adhesive organs. A similar strand of epidermis from which epidermal vesicles separate off into the dorsal test above the endostyle is on each side of the mid-dorsal line behind the adhesive organs. The tail winds about two-thirds of the distance around the trunk. The lateral ampullae separate from the rest of the larval ectoderm and become large and spherical.

REMARKS

In those colonies with male follicles clumped in the posterior end of the zooid, the anterior part of the posterior abdomen is relatively narrow, resembling the neck of a polyclinid posterior abdomen. However, the species has characters of *Synoicum* rather than *Polyclinum*, viz. the mid-intestine is large and inflated, the gut loop straight and relatively long, and the cloacal systems small.

Synoicum clavatum (Oka, 1927) from Japan resembles the present species in some characters, but it differs in having larger round-topped rather than flat-topped lobes with longer, narrow stalks. There is some confusion regarding the characters of the Japanese species, however, for Nishikawa (1990) records 20 to 24 longitudinal muscles and 10 to 12 stigmata, but Tokioka (1954b) reported only 12 muscles and 20 stigmata (see Tokioka 1954b, Pl. IVF). The colours of living colonies of the Japanese populations, which could provide more evidence of their relationships with one another and with the present species, have not been recorded.

Synoicum clavatum: Millar, 1975 from the Philippines has flat-topped lobes containing circular cloacal systems similar to those of the newly recorded Australian material; and the zooids have 8 to 9 longitudinal muscles similar to those from Heron I. However, although they are in 15 rows like the Australian material, Millar reports about 20 stigmata per row in his specimens. The flat-topped Philippine colonies, therefore, are only questionably conspecific with the Australian colonies. The dorsal papilla has not been recorded for Philippine or Japanese specimens. *Synoicum kuranui* Brewin, 1950b from Great Barrier I. (New Zealand) are sandy capitate lobes with crimson zooids and areolated stomach walls and are readily distinguished from the present species. *Synoicum kuranui*: Kott, 1963 from Heron I. is not conspecific with either the present one or with the New Zealand species (see *S. durum*, above). The sympatric *S. intercedens* has sessile cushion-like colonies with sandy margins. Their upper surface with swellings corresponding to the systems, larger systems, longer atrial tongues, a mulberry-like stomach and a smaller larva.

Synoicum suarenum is a tropical species and it differs from the temperate *S. sacculum* by the shape of the colony lobes (sessile in *S. sacculum*), the smooth stomach wall (mulberry-like in *S. sacculum*), and the small, almost rudimentary cloacal systems with the wide cloacal aperture exposing the cloacal cavity to the exterior, as in some *Eudistoma* spp. (*angolanum* group: Kott 1990).

Synoicum tropicum (Sluiter, 1909)
(Fig. 57)

Atopogaster tropicum Sluiter, 1909, p.107.

DISTRIBUTION

NEW RECORD: Western Australia (NW Shelf, QM GH5056).

PREVIOUSLY RECORDED: Indonesia (Sluiter 1909).

The species is known only from the type and from the newly recorded portion of a colony.

DESCRIPTION

EXTERNAL APPEARANCE: The specimen is a wedge-shaped slice of what appears to have been a large, upright lobe, about 12cm high. The test is firm and the surface naked.

Zooids are arranged in circular systems of 8 to 20. The branchial apertures are around the margin of a circular depression about 5mm diameter in the surface test. A conspicuous common cloacal aperture protrudes on a conical prominence in the centre of each circle of zooids. The test is white and opaque, with a patch of dark pigment where each zooid opens to the surface. Common cloacal apertures are about 7mm apart, an area of test without zooid openings separating the circles of branchial apertures from one another.

INTERNAL STRUCTURE: The zooids in the present piece of a colony have not been adequately fixed and cannot be dissected or manipulated without disintegrating. They are, as in the type specimen, perpendicular to the surface. The zooids of the type colony (Sluiter 1909) have 12 rows of 8 to 10 stigmata. The gut forms a simple loop, the stomach wall is smooth, and there is a long posterior abdomen.

REMARKS

The present specimen agrees with the type in having circular depressions on the surface with

branchial apertures around the margin of each depression, protruding cloacal apertures, and no sand either embedded or adhering to the surface. The circular surface depression is characteristic. Although circular systems with a large circular cloacal cavities surrounded by zooids occur in other species of *Synoicum*, the well-spaced and depressed circles of the present species are unusual.

The horizontal stomach folds that characterised the genus *Atopogaster* (to which Sluiter assigned this species), are artefacts that occur in species with large, smooth stomachs and *Atopogaster* is here proposed as a junior synonym of *Synoicum*.

Genus **Morchellium** Giard, 1872

Type species: *Amaroucium argus* Milne Edwards, 1842.

The known species have a relatively long oesophagus. A vertical, barrel-shaped stomach halfway down the abdomen is smooth or has mulberry-like swellings in the stomach wall. Gonads are in the posterior abdomen with the ovary anterior to the serially arranged testis follicles. Rows of stigmata are numerous. The atrial aperture is wide and open, often forming a protuberant siphon with an enlarged uppper rim. Neither the atrial lip nor the sphincter muscle are as well developed as they are in *Aplidium* and *Polyclinum*. The posterior abdomen is narrow and continuous with the abdomen, there being no constriction between them.

The number of rows of stigmata are in the range known for other genera of the Polyclinidae. However the number per row (20 to 30) generally exceeds that of all other genera of this family, being almost as numerous as in Polycitoridae and *Sigillina* spp. The number of stigmata per row in Protopolyclinidae, and in some *Ritterella* spp., are of this order. In Euherdmaniidae and Placentelidae they are more, and in Pseudodistomidae less numerous.

Although they are not present in the type species, the Australian species of this genus have parastigmatic vessels in the branchial sac. A few species of *Aplidium* — e.g. *A. caeruleum* (Sluiter, 1906) — and *Synoicum atopogaster* also have parastigmatic vessels (see Kott 1969) and so do certain Protopolyclinidae (*Monniotus* spp., *Condominium*) and certain *Ritterella* spp. (see above)

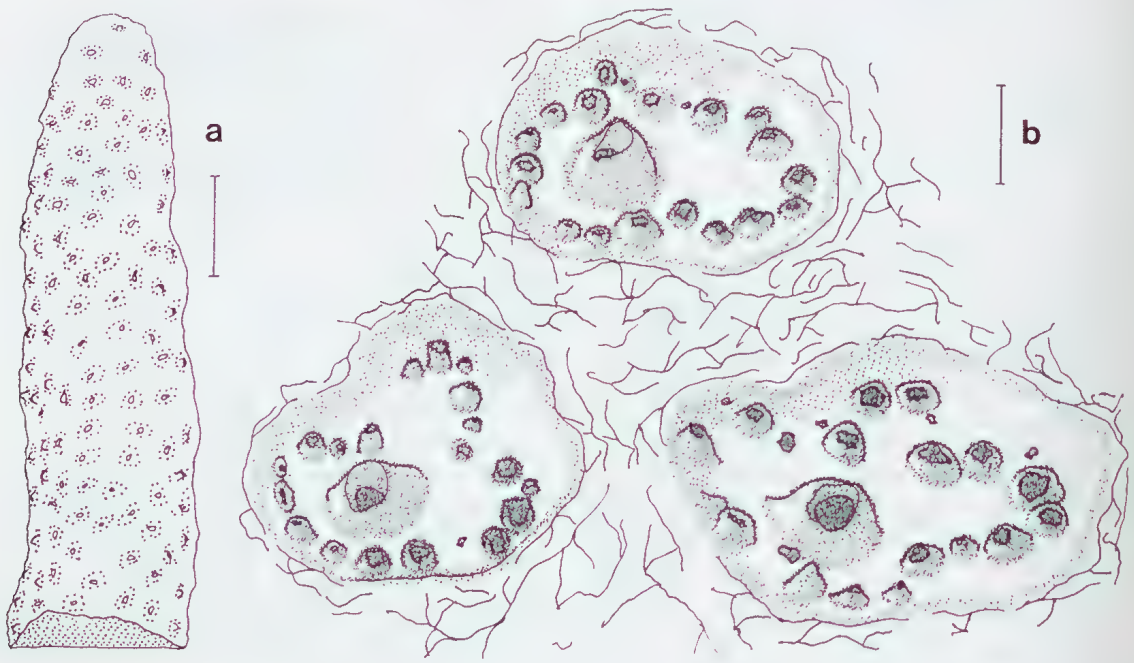


FIG. 57: *Synoicum tropicum* (QM GH5056) — **a**, part of colony; **b**, circular systems with protuberant branchial apertures surrounding a larger, central common cloacal aperture, each depressed into the surface. Scales: **a**, 2cm; **b**, 2mm.

as well as holozoid genera *Distaplia*, *Sycozoa* and *Hypsistozoa*. Thus no profound phylogenetic significance can be attached to the presence of these vessels in *Morchellium* species. Parastigmatic vessels hold in place the long, parallel interstigmatic bars that occur in most species with particularly long, narrow stigmata. These generally occur when there are few rows of stigmata relative to the size of the branchial sac. Probably the presence of parastigmatic vessels, preventing distortion of the stigmata, maintaining the dimensions of their apertures and the effective operation of the cilia lining them, is a convergent character in the taxa referred to above.

The transverse thoracic muscles of the Australian species *M. pannosum* n.sp. are unique in the Polyclinidae, although they are known in *Sigillina* (Holozoidae), Polycitoridae (see Kott 1990) and some Ritterellidae (see above). The pigment spots in each of the branchial lobes (as in the Diazonidae and *Euherdmania* spp.) are also unsual. Neither of these characters occurs in *M. albidum* n.sp. Thus, they do not seem to be generic characters as the genus is currently defined. Nor do they occur in *Synoicum*.

Morchellium argus (type species) has 4 symmetrically arranged unusual pigment spots around the apertures (Berrill 1950), but these are not homologous with the diazonid-like pigment spots of *M. pannosum* n.sp.

The large atrial aperture, and barrel-shaped stomach without longitudinal folds found in both Australian species are similar in certain *Synoicum* spp. from which *Morchellium* is distinguished only by its 8 branchial lobes.

The type species is from the English Channel and the west coast of Britain, Ireland and France.

The species discussed below are the only 2 of this genus described from Australia. They differ from one another principally in their colonies, *M. pannosum* n.sp. having sandy lobes, each with a single system, and *M. albidum* n.sp. having numerous circular systems in each cushion-like colony.

Morchellium partitionis (Monniot, 1987) from New Caledonia, the only species of thus genus previously recorded from the tropical western Pacific, is divided into sandy claviform lobes and is 2cm high. The external test is thickly encrusted with sand. Its colony form is similar to that of *M. pannosum* n.sp., and it has a similar number of rows of stigmata (13 to 14) and a similar number of stigmata per row (18). However its lack of parastigmatic vessels and its mulberry-like stomach distinguish it.

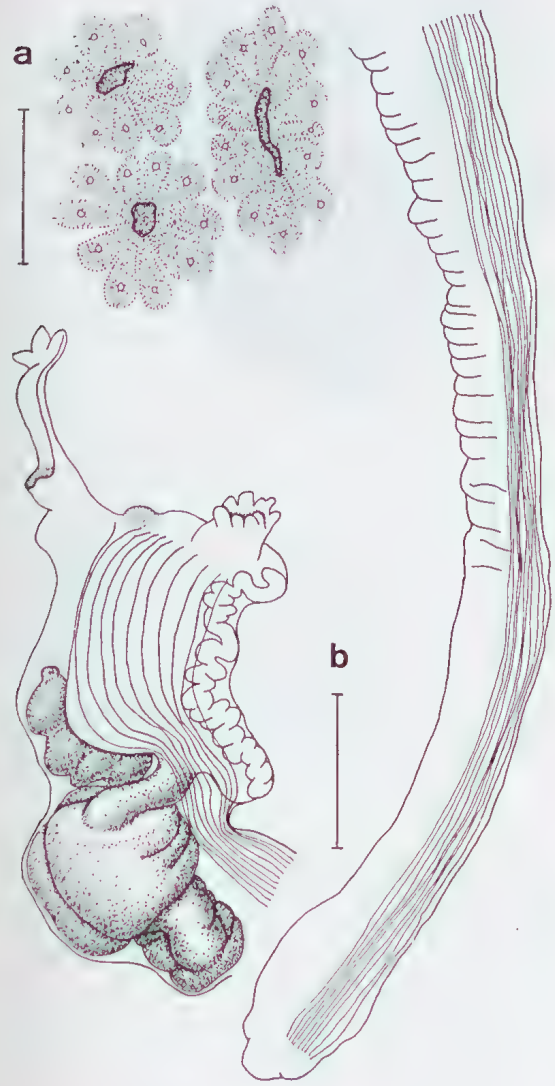


FIG. 58: *Morchellium albidum* n.sp. (holotype QM GH5582) — **a**, part of upper surface showing zooid systems; **b**, zooid, with detached posterior abdomen showing ventral muscle band. Scales: **a**, 4mm; **b**, 0.5mm.

Morchellium albidum n.sp.
(Fig. 58)

DISTRIBUTION

TYPE LOCALITY: South Australia (West Bay, Wedge I., southern Spencer Gulf, Earthwatch site 2, coll. A. Butler 16.2.88 QM GH5582).

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: The colony is a large, oval bolster 4cm long and 3cm wide. Zooids are arranged in crowded, circular systems of up to 12, with large sessile common cloacal apertures in the centre of each. The test is firm and transparent and the zooids, seen clearly from the surface, are translucent-white in preservative. An opaque white deposit is in the surface test between the systems.

INTERNAL STRUCTURE: Zooids are large and robust. However, the thorax and abdomen together are as little as 1.4mm long when contracted. The posterior abdomen is longer. The rim of the branchial aperture has 8 conspicuous rounded lobes. The atrial aperture protrudes from the dorsal surface, and its anterior rim is sometimes produced into a strap-like tongue, with 3 pointed terminal lobes. In other specimens the atrial lip is shorter and broader, the 3 terminal lobes being more conspicuous than the tongue itself. A median dorsal papilla is present behind the aperture. The thorax has about 12 longitudinal muscles which form a wide band along the ventral border of the abdomen and posterior abdomen. When contracted this ventral band draws the posterior abdomen up alongside the abdomen.

Stigmata are in about 12 rows of probably up to 12, but the thorax is too contracted to allow accurate counts to be made. Each row of stigmata is crossed by a parastigmatic vessel.

The stomach is voluminous, and collapsed into irregular, more or less horizontal folds. The posterior abdomen is about the same length as the rest of the zooid. It contains a double series of male follicles and an ovary anterior to these.

REMARKS

The zooids of this species resemble those of *Morchellium pannosum* n.sp., as well as *Synoicum atopogaster* and *S. concavitum*. The naked bolster-like colonies differ from all these except the last, which, however, has firmer test, less crowded systems, and lacks parastigmatic vessels. The present species also has fewer rows of stigmata, and fewer per row than *Synoicum atopogaster* or *Morchellium pannosum* n.sp.

Morchellium pannosum n.sp.
(Fig. 59)

DISTRIBUTION

TYPE LOCALITY: Victoria (Port Phillip Heads, 18m, fast current, coll. J. Watson 10.9.77, holotype QM G12722).

The species is said to be common off Port Phillip Heads.

DESCRIPTION

EXTERNAL APPEARANCE: The newly recorded specimen is an irregular mass of sandy test, up to 3cm high, with the upper half of the colony divided into flattened to cylindrical lobes about 1cm in diameter.

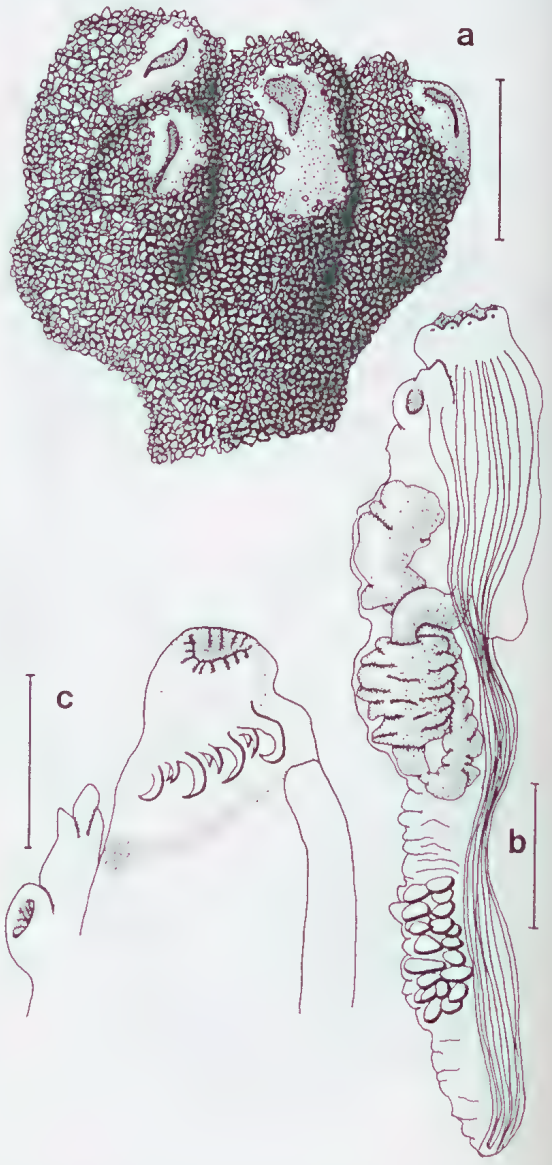


FIG. 59. *Morchellium pannosum* n.sp. (holotype QM G12722) — **a**, part of colony; **b**, whole zooid; **c**, anterior part of zooid showing atrial lip, atrial aperture, branchial aperture and tentacles, and position of neural complex. Scales: **a**, 5mm; **b**, 1mm; **c**, 0.5mm.

A bare area with a large usually long, narrow opening in the centre is on the upper surface of each of the lobes, which contain single, or occasionally 2 cloacal systems. The cloacal cavities are relatively shallow.

The test is very soft, jelly-like, flaccid and translucent. Internally, sand is present in the base of the colony, but not elsewhere. The living zooids are reported to have been mauve.

INTERNAL STRUCTURE: The zooids are robust. About 20 strong longitudinal muscle bands on the thorax extend along on each side of the ventral line of the abdomen and posterior abdomen in 2 wide bands. On the thorax there also appears to be a layer of transverse muscle fibres over the longitudinal thoracic bands. In these contracted zooids (about 6mm long), the abdomen is shorter than the thorax, which is about the same length as the posterior abdomen. The latter curves ventrally as a result of the strong ventral longitudinal bands.

The rim of the branchial aperture appears to have 8 very shallow lobes in which there are faded pigment spots, although in some contracted specimens the rim looks puckered and gathered rather than lobed. A fleshy tridentate lip extends out from the upper rim of the atrial aperture. There are about 16 branchial tentacles of about 3 size groups, each group in a circle at slightly different levels in the base of the branchial siphon. About 15 rows each of about 20 long stigmata are folded along a parastigmatic vessel. The stomach is large, smooth-walled, and has irregular transverse folds that probably result from its collapse. The duodenum is moderately long, and a posterior stomach is in the bend of the gut loop. The voluminous rectum extends halfway up the thorax. A double row of male follicles are in the middle of the posterior abdomen.

REMARKS

In addition to the number of branchial lobes, the species distinctive characters are its fleshy body wall, strong (including transverse) muscles, roomy, transversely folded stomach, parastigmatic vessels, and distinctive lobed colony with flaccid test and large naked cloacal apertures.

The transversely folded stomach is similar to that of *Synoicum atopogaster* and *S. tropicum* (Sluiter, 1909). It was previously thought to be characteristic of the genus *Atopogaster* (< *Synoicum*).

Zooids resemble those of *Synoicum atopogaster* Kott, 1963 which has a similar number of stigmata, parastigmatic vessels and longitudinal muscles that draw the posterior abdomen up alongside the abdomen. The present species is distinguished by its 8 branchial lobes and their associated pigment spots, transverse thoracic muscles and single cloacal system per lobe.

Genus **Aplidium** Savigny, 1816

Type species: *Aplidium lobatum* Savigny, 1816.

Zooids usually are small and thread-like with a relatively, narrow thorax and gonads in a posterior abdomen that is continuous with (rather than constricted off from) the abdomen. There are 6 or sometimes 8 branchial lobes. The atrial tongue is relatively small and rises from the anterior rim of the opening or from the body wall anterior to it. The atrial cavity also is relatively small. Longitudinal muscles extend the length of the thorax and continue onto the abdomen and posterior abdomen. Transverse muscles are in the transverse branchial vessels, joining with the longitudinal muscles in the parietal body wall through atrial connectives. The gut loop is vertical with a vertical rather than curved oesophagus and a vertical barrel-shaped stomach with parallel longitudinal folds in its wall. In *Aplidium*, like *Synoicum*, but unlike *Polyclinum*, *Aplidiopsis*, and other families of Aplousobranchia with a short abdomen, the post-duodenal or proximal part of the mid-intestine — between the duodenum and posterior stomach — has more or less the same diameter as the duodenum rather than being narrower. A short distal section of mid-intestine lies between the oval posterior stomach (which usually is in the bend of the gut-loop) and the rectum. Often there are small pockets (caeca) each side of the proximal end of the rectum, and these form a rectal valve. The anus opens one third to halfway up the atrial cavity.

Larvae are small, the trunk usually less than 1mm and most often less than 0.8mm. Three small, shallow adhesive organs on long slender stalks are present in the anterior mid-line. Median and lateral ectodermal ampullae sometimes are present anteriorly, and usually there are ectodermal vesicles at the anterior end of the trunk. These are 2, 3 or more deep in a wide band, or in a single series, forming an arc along each side of the median adhesive organs. Sometimes they also occur in the median line between the adhesive organs (Fig. 60). The vesicles separate from, or sometimes remain directly attached to the ectoderm by, fine, sometimes branched, stalks. This

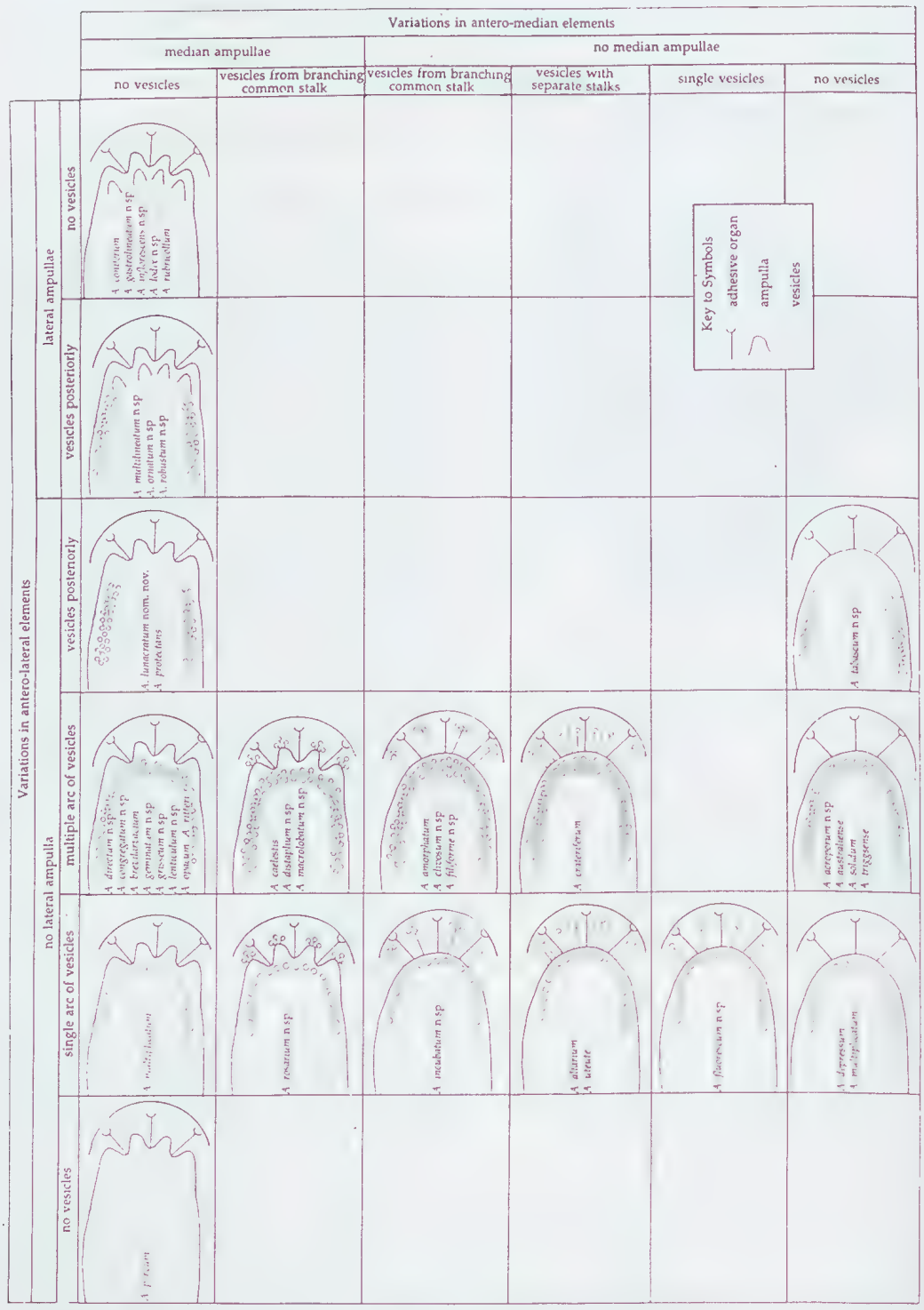


FIG. 60. Epidermal elements of the anterior end of the larval trunk in *Aplidium* spp. (showing their relative position, but not their precise number for any one species; diagrammatic).

constitutes a distinction from *Polyclinum* in which the only vesicles are those that branch off long strands of ectoderm which trail back through the larval test, one on each side of the mid-dorsal and mid-ventral lines and form postero-ventral and antero-dorsal patches of vesicles. These patches of vesicles occasionally also occur in *Aplidium*, but are seldom the only ones present. As in *Polyclinum*, the larval ocellus and otolith in *Aplidium* are well developed.

Colonies often are large, but appear to be well integrated, with zooids organised into cloacal systems and with an external morphology of the colony that enhances its interactions with the external environment. Thus, branchial openings may be protected in depressed parts of the surface test, at the base of ridges or swellings of the surface test (e.g. *A. caelestis*, *A. crateriferum*). Cloacal apertures usually are elevated above the colony on conical prominences (Kott 1989). The test of *Aplidium* is gelatinous, but often is relatively firm, and sometimes is further strengthened by dense inclusions of embedded sand. Many species appear to sort the sand embedded in the test, large sand particles being found in the base and margins of the colony while smaller particles are around the branchial and cloacal apertures, where the test could be expected to be more flexible.

The cloacal cavities generally are shallow, with only a thin layer of surface test over them. Atrial apertures always are at the anterior end of the dorsal surface, and variations in their position usually are a result of contraction of body musculature. Deeper cloacal cavities sometimes develop, and the atrial opening into the base of the cloacal cavity with the atrial lip inserted above it is accommodated by the separation of the atrial lip from the aperture. Thicker surface test is accommodated by a long branchial siphon (e.g. *A. crateriferum*).

The genus *Sidnyum* Savigny, 1816 (type species *Sidnyum turbinatum* Savigny, 1816) is distinguished from *Aplidium* only by the 8-lobed (rather than 6-lobed) branchial apertures. The zooids form circular systems which open on the upper surface of soft, cushion-shaped or lobed colonies with translucent test, and with or without encrusting sand. The best known species of this genus are the type and the related *S. elegans* (see Berrill 1950), which both are common in some European locations. In addition to the 2 related European species, the known species with usually (but not always) 8 branchial lobes are:

Synoicum appendiculatum Michaelsen, 1923 from the Azores. Although assigned to *Sidnyum* by Monniot (1974), the species with its deeply curved oesophagus bilaterally symmetrical stomach with furrows (rather than folds), seems appropriately placed in the genus *Synoicum*.

Sidnyum pentatrema Monniot, 1972 from Bermuda and Guadaloupe (see Monniot 1983) appears to be an *Aplidium* species in which the number of branchial lobes varies from 6 to 9, although 8 is the number which occurs most often (Monniot 1972, 1983). These lobes are not equal in size, and probably several have subdivided to produce the higher number, which accordingly cannot be said to represent a reliable plesiomorphic character indicating generic status for the taxon.

Sidnyum pentatrema: Monniot and Monniot, 1987, known only from 2 small sand covered lobes from French Polynesia probably is convergent rather than conspecific with the Azores species.

Aplidium mernooensis (Brewin, 1956) from Chatham I., New Zealand has characters in common with both *S. pentatrema* and *S. appendiculatum*. Monniot (1972) concluded that *S. appendiculatum* from the Azores is distinct from *A. mernooensis*, but the relationships between the latter and the Tahitian *S. pentatrema*: Monniot and Monniot, 1987 and *A. mernooensis*: Monniot, 1987 from New Caledonia are not clear (see *A. filiforme* n.sp., below).

Aplidium amorphatum Kott, 1963 and *A. protectans* (Herdman, 1899) have (see below) 8 branchial lobes. Their other characters (including the stomach folds) conform with the genus *Aplidium*.

Sidnyum indicum Renganathan and Monniot, 1984, a massive gelatinous colony from the Indian Ocean, has thread-like zooids that have the usual characteristics of *Aplidium* including a folded stomach (see *A. protectans*, below).

Thus, of the 8 species that are possible candidates for the genus *Sidnyum*, 3 — *S. pentatrema* Monniot, 1972; *S. pentatrema*: Monniot and Monniot, 1987; and *A. mernooensis* (Brewin, 1956) — with 5 rows of stigmata and 5 stomach folds, probably are the result of convergent evolution. The number of branchial lobes in at least one of these species is unstable. The species appear at least as closely related to species of *Aplidium* as to one another. Of the other 5 known species, the 2 closely related and sympatric European ones do not seem to have closer relationships with the Australian *A. amorphatum* and *A. protectans*, and the Indian Ocean *A. indicum* than with other *Aplidium* species.

Further, in the diverse genus *Aplidium*, both adult and larval morphological differences between species and groups of species appear to

transcend (in evolutionary terms) the few differences between *Sidnyum* and *Aplidium*. Accordingly, in this work the genus *Sidnyum* is considered a synomym of *Aplidium*.

Aplidium has a close relationship with *Synoicum*. The difference between them disappears when, in some *Aplidium* species, the stomach wall is distended and the 5 folds flatten out. Further the larvae are similar, and it is probable that these two polyclinid genera are closely related phylogenetically.

Resolution of the taxonomy, and identification of species of the genus *Aplidium* has been, and continues to be, a problem. Owing to post-mortem changes and other artefacts of fixation and preservation, the reported appearance of living specimens is often difficult to reconcile with their changed appearance in preservative. In the preserved specimens, systems often are obscured by sand, and colours oxidise or are lost altogether. Zooids, already small and convergent, contract and withdraw from the surface, thus obscuring both their morphology and their arrangement in opaque and often distorted colonies. This confusion is compounded by a degree of plasticity in the shape of colonies which grow to accommodate a variety of substrates and conditions. Further the number of specimens available for examination does not always include a range of age groups or material from a variety of populations so that intraspecific variation is often not known, or has not been recognised. Difficulties also exist in finding reliable taxonomic characters in these small, simplified zooids, and in their crowded colonies.

The number of rows of stigmata, stomach folds, stigmata per row, and the configuration of the atrial aperture and lip, are important characters for species identification. Also of significance are characters of the colonies such as the distribution of pigment, consistency of the test, distribution and nature of test inclusions, form of the systems, shape of the colony and the presence or absence of a stalk. Usually of only limited significance at the species level are the relative lengths of different parts of the zooid (especially the posterior abdomen), the number of longitudinal muscle bands and the number and arrangement of testis follicles, which either are affected by the flexibility and contractability of the zooids, or by variations in form that occur with growth and sexual maturity.

In identifying species of this genus, particular care needs to be paid to the counting of stomach folds. The whole thickness of the stomach wall is pleated, and accordingly folds are internal as well as external. Internal pleats seen through the wall and counted with the external ones may explain the high intraspecific variation in the number of folds sometimes recorded. A transverse section of the stomach enables accurate counts to be made. The number of rows of stigmata is obscured when a part or the whole of the branchial sac is contracted. Inaccurate counts of the number of rows and the number per row occur when, in contracted sacs, stigmata are folded, and the interstigmatic bars and the perforations are crowded together. Fully relaxed branchial sacs are desirable for accurate determination of their structure, and dissection to expose the stigmata is essential, as shadows seen through the contracted body wall are not a reliable way to count the rows.

Nishikawa (1990) points out that the genus *Aplidium* is one of the largest in the Ascidiacea. *Aplidium* species abound in temperate as well as tropical seas. Because of the difficulties in resolving the taxonomy of species in this genus some of the approximately 200 recorded may be invalid. Others have been lumped together, more critical examination showing that many previously considered conspecific taxa are actually distinct from one another.

Most of the previous works on the *Aplidium* fauna of Australia are based on relatively small collections from limited areas, viz. from New South Wales (Herdman 1899), northwestern Australia (Hartmeyer 1919, Millar 1963), south-western Australia (Michaelsen 1930), Port Phillip Bay (Millar 1966), eastern and north-eastern Australia (Herdman 1886, Herdman and Riddell 1913, Kott 1966, 1972c), South Australia (Kott 1972a,b, 1975 and 1976). Kott (1963) dealt with Australia-wide collections. Sluiter (1909) in his report on the Siboga collection encountered only 5 species of *Aplidium* of which 4 occur in Australia. Only 25 species of *Aplidium* spp. have previously been reported from Australia.

The number of specimens available for examination in the present study has made it possible to more accurately determine species parameters and resolve synonymy. The identity of most of the 16 previously known indigenous Australian species and the 4 recorded also from the Western Pacific has been confirmed, however the 2 species said to be conspecific with species recorded from New Zealand, 3 from South Africa, and a pantropical species (*A. lobatum*), were wrongly assigned. No *Aplidium* species has been found to have a range from Australia to either South Africa or New Zealand, and the number of apparently

indigenous Australian species has been significantly increased as a result of the present review.

Aplidium, with 46 known species, including a relatively high indigenous component, now recorded from Australia, is one of the most diverse genera of the Ascidiacea in these waters (Tables 7–9).

Key to species of *Aplidium* recorded from Australia

1. Stomach folds more than 8 2
   Stomach folds not more than 8 25

2. Cloacal apertures few and terminal or central; parallel longitudinal or radial cloacal canals 3
   Cloacal apertures numerous and scattered over the colony surface; no long, parallel longitudinal or radial cloacal canals 9

3. Colonies flat-topped sandy lobes adhering to one another ..... *A. congregatum* n.sp.
   Colonies not flat-topped sandy lobes adhering to one another 4

4. Colony with thin, leathery stalk. *A. australiense*
   Colony without thin leathery stalk 5

5. Stomach folds less than 20 6
   Stomach folds more than 20 7

6. Stomach folds 10 ..... *A. brevilarvacium*
   Stomach folds more than 10 ..... *A. parvum*

7. Colony sessile or top-shaped, without a stalk... ..... *A. altarium*
   Colony not sessile or top-shaped, with a stalk..8

8. Head of colony with sand externally; larval trunk with epidermal vesicles ..... *A. geminatum* n.sp.
   Head of colony without sand externally; larval trunk without epidermal vesicles ..... *A. inflorescens* n.sp.

9. Stigmata in 5 rows 10
   Stigmata in more than 5 rows 11

10. Atrial aperture with a lip .. *A. minisculum* n.sp.
    Atrial aperture without a lip ..... *A. depressum*

11. Zooids in long conspicuously branching double-row systems 12
    Zooids not in long conspicuously branching double-row systems 14

12. Sand embedded throughout ..... *A. elatum*
    Sand not embedded throughout 13

13. Branchial siphon surrounded by wide band of white, opaque cells; larvae with single series of epidermal vesicles each side of anterior mid-line ..... *A. multiplicatum*
    Branchial siphon not surrounded by wide band of white, opaque cells; larvae with multiple series of epidermal vesicles each side of anterior mid-line ..... *A. opacum*

14. Stomach folds not more than 15 15
    Stomach folds more than 15 17

15. Sand embedded in the test 16
    Sand not embedded in the test ..... *A. fluorescum* n.sp.

16. Sand embedded in surface layer of test; zooids in conspicuous circular systems .... *A. jacksoni*
    Sand embedded in basal layer of test; zooids not in conspicuous circular systems ..... *A. triggsense*

17. Stigmata more than 20 per row; brood pouch present ..... *A. uteute*
    Stigmata less than 20 per row; brood pouch not present 18

18. Stigmata in more than 12 rows 19
    Stigmata in 12 rows or fewer 21

19. Stomach folds 18; stigmata not more than 8 per row ..... *A. gelasinum* n.sp.
    Stomach folds 20 or more; stigmata more than 8 per row 20

20. Stomach folds oblique ..... *A. gastrolineatum* n.sp.
    Stomach folds not oblique ..... *A. robustum* n.sp.

21. Stomach folds 30, oblique ..... *A. multilineatum* n.sp.
    Stomach folds less than 30, not oblique 22

22. Systems circular 23
    Systems not circular ..... *A. rosarium* n.sp.

23. Sand on upper surface of colony ..... *A. incubatum* n.sp.
    Sand not on upper surface of colony 24

24. Stigmata more than 10 per row ... *A. lodix* n.sp.
    Stigmata not more than 10 per row ..... *A. ornatum* n.sp.

25. Atrial lip separate from rim of aperture 26
    Atrial lip not separate from rim of aperture .35

26. Colonies undivided, upright and regular 27
    Colonies not undivided, upright and regular 26

27. Colony sandy externally ..... *A. magnilarvum* n.sp.
Colony not sandy externally ..... *A. coniferum*

28. Systems circular 29
Systems not circular 31

29. A single system per colony lobe ... *A. directum*
More than a single system per colony lobe . 30

30. Branchial siphon with bulging branchial sphincter ..... *A. crateriferum*
Branchial siphon without bulging branchial sphincter ..... *A. lunacratum* nom. nov.

31. Cloacal systems irregular; cloacal apertures at junction of 2 or 3 canals 32
Cloacal systems regular; cloacal apertures in centre of radially converging canals 33

32. Common cloacal canals surround circular to polygonal zooid-free areas ..... *A. lenticulum* n.sp.
Common cloacal canals do not surround circular to polygonal zooid-free areas ..... *A. caelestis*

33. Stomach folds 5 34
Stomach folds 8 ..... *A. griseum* n.sp.

34. Stigmata in 18 rows ..... *A. clivosum* n.sp.
Stigmata in 12 rows ..... *A. rubricollum*

35. Stigmata in 4 or 5 rows 36
Stigmata in more than 5 rows 39

36. Colony a 3 dimensional reticulum; 8 stomach folds ..... *A. acroporum* n.sp.
Colony not a 3 dimensional reticulum; 5 stomach folds 37

37. Stigmata in 4 rows ..... *A. distaplium* n.sp.
Stigmata in 5 rows 38

38. Stalks long; one system per terminal branch ..... *A. bacculum* n.sp.
Stalks not long; more than one system per terminal lobe ..... *A. filiforme* n.sp.

39. Sand sparse or absent from internal test 40
Sand moderate or crowded in internal test .. 42

40. Branchial lobes 8 41
Branchial lobes 6 .... *A. parastigmaticum* n.sp.

41. Parastigmatic vessels present .... *A amorphatum*
Parastigmatic vessles not present ..... *A. protectans*

42. Colony a single system . *A. paralineatum* n.sp.
Colony not a single system 43

43. Stigmata more than 10 per row ..... *A. macrolobatum* n.sp.
Stigmata less than 10 per row 44

44. Cloacal canals surround extensive irregular patches of zooid-free test; systems not crowded; embedded sand not crowded ..... *A. tabascum* n.sp.
Cloacal canals do not surround extensive irregular patches of zooid-free test; systems crowded; embedded sand crowded 45

45. Cloacal canals surround small circular zooid-free areas 46
Cloacal canals surround narrow zooid-free ridges ..... *A. ritteri*

46. Larva with median ampullae; southern Australian ..... *A. petrosum* n.sp.
Larvae without median ampullae; not southern Australian ..... *A. solidum*

Species recorded from waters adjacent to Australia

Aplidium cellis Monniot, 1987 has double rows of zooids around raised zooid-free areas of test as in *A. tabascum* n.sp., from which the species is distinguished by its smaller larva (less than 0.6mm trunk) and the sand which is said to completely encrust the surface, albeit it is less crowded over the cloacal canals. Although the colony resembles *A. lenticulum* n.sp. the zooids differ, having the atrial lip from the upper rim of the opening, similar to the zooids of *A. ritteri* (> *A. lobatum*: Monniot, 1987). The species may be conspecific with *A. lobatum* Savigny (see below).

Aplidium flavolineatum: Monniot 1987, from the Coral Sea, has zooids (with brood pouch, large thorax and short posterior abdomen), and possibly also the larvae (with epidermal vesicles around each adhesive organ attached to the epidermis by narrow stalks) like those of *A. altarium*. *Aplidium altarium* has only a limited number of systems in each colony, each consisting of double rows of zooids converging to central or terminal cloacal apertures. The Coral Sea specimen has circular systems and a brood pouch like *A. uteute*. However, the latter species has more numerous lateral vesicles in the larval trunk.

Aplidium lobatum Savigny, 1816 from the Gulf of Suez, later (as *A. africanum* Sluiter, 1905) reported from the Gulf of Aden, is said to be irregularly lobed but small (5 to 6mm thick), with yellowish white zooids in lines amongst the sand embedded in the transparent test. The upper surface is divided into flat-topped oval cushions which have deep furrows surrounding them. The cloacal canals into which the zooids open are in these furrows. Sand does not

adhere externally, stigmata are in 9 or 10 rows of about 12, the trifid atrial lip is part of the anterior rim of the aperture. The posterior abdomen is short, the male and female gonads are not present in the same zooid at the same time and the larval trunk is 0.5mm long (Michaelsen 1920). In his review of the species, Michaelsen added records from the Mediterranean (through the synonymy of *A. tremulum* Savigny, 1816), and suggested a range extending to Malaysia and Indonesia through synonymy with *Aplidium tremulum*: Sluiter, 1909. However, this requires confirmation as most assignations from the western Pacific by Tokioka (1967), Nishikawa (1984a), Monniot (1987) and Monniot and Monniot (1987) appear to be synonyms of *A. ritteri* (see below). *Aplidium lobatum*: Kott, 1963 is conspecific with *A. macrolobatum* n.sp. *Aplidium tabascum* n.sp. and *A. cellis* Monniot, 1987, with smaller lobes on the apertures, and elevated cushions surrounded by depressions into which the zooids open, have both colony and zooids like *A. lobatum* from Suez. Particularly *A. cellis*, with its embedded sand and small larva, is indistinguishable.

The small specimens from the Marianas (*A.* aff. *lobatum*: Tokioka, 1967), with the atrial lip separate from the aperture, is not this species. It is similar to *A. caelestis* or *A. nadaense* Nishikawa from Japan. Atlantic specimens assigned to *A. lobatum* (see Van Name, 1945) have fewer rows of stigmata than the types, the colonies are different, and they probably are not conspecific with the Red Sea specimens. Their similarity could well be the result of convergence.

Aplidium maru Monniot and Monniot, 1987, from French Polynesia, has a larva with median ampullae and, on each side, a band of lateral epidermal vesicles at the anterior end of the trunk (see Fig. 60). There is no other species in the group with similar larvae which also has circular to oval systems of zooids arranged around a protuberant cloacal aperture, 5 stomach folds and an atrial lip separate from the opening.

Aplidium mernooensis (Brewin 1956) from the subantarctic Chatham I., New Zealand (see also Millar 1982) is reported from the tropical New Caledonian waters by a single colony (Monniot 1987). The colony has sand externally but not internally. Its upper surface is lobed, each lobe containing a single circular system. Zooids have red thoraces, with 8 branchial lobes, 5 stomach folds and 5 rows of stigmata. The occurrence of this species in a tropical location is surprising and the identity of the New Caledonian specimen requires confirmation, especially in view of the possibility of convergence in species with zooids as small as these. The New Zealand specimens have almost twice as many stigmata as *A. filiforme* n.sp. (see below). The larvae of both the Chatham I. and New Caledonian specimens are larger than *A. filiforme* n.sp., but they are otherwise all similar to one another.

Aplidium multipapillatum Millar, 1975 from Hong Kong and New Caledonia (Monniot 1987) is characterised primarily by its larvae with 5 adhesive organs.

Aplidium nadaense (Nishikawa, 1980), a species probably indigenous to Japan has the atrial lip separate from the aperture, 13 to 15 rows of up to 8 stigmata, and 5 stomach folds. The colony is smooth-surfaced and the systems are not as conspicuous as they are in *A. caelestis*. Monniot and Monniot (1987) and Monniot (1987) assigned specimens, from French Polynesia and New Caledonia respectively, to this species. *Aplidium nadaense*: Monniot, 1987 from New Caledonia has 14 to 16 rows of stigmata, but branchial apertures are in furrows in the surface, between small polygonal areas, resembling *A. solidum*, which, however, does not have the atrial lip separated from the aperture. *Aplidium nadaense*: Monniot and Monniot, 1987 has a longer, narrower zooid but fewer rows of stigmata than the type. Neither the number of stigmata per row nor the form of the systems is reported. The small larva and other features of the zooid are similar to *A. lobatum*, but the long narrow posterior abdomen is not. Probably neither *A. nadaense*: Monniot 1987 nor *A. nadaense*: Monniot and Monniot 1987 are conspecific either with the Japanese species or any known Australian ones.

Aplidium uouo Monniot and Monniot, 1987 from French Polynesia resembles *Aplidium ritteri* in its long, winding systems, atrial lip from the upper border of the apertures, 10 rows of about 6 stigmata, 5 stomach folds, short posterior abdomen containing gonads of only one sex at a time, and a larva without median vesicles or ampullae and a band of lateral vesicles. It is distinguished only by the absence of embedded sand usually associated with *A. ritteri*, the band of lateral vesicles is not as wide, and the larval trunk (0.7mm long) is longer than that of *A. ritteri*.

Aplidium acroporum n.sp.
(Fig. 61. Plate 10a,b)

DISTRIBUTION

TYPE LOCALITY: South Australia (The Gap, near Thistle I. Spencer Gulf, coll. S. Shepherd 8.4.87, holotype SAM E2554 *QM GH4169*; Horseshoe Reef near Kingston, 36°35.0'E, flat rock platform, small overhang, sand patches 20m, coll. R. McCauley 17.2.89, paratype QM GH5443; Kangaroo I, Cape D'Estaing, Emu Bay north of reef, 35°34.3'S 137°30.2'E brown algae covered rocks merging to sand and sea grass 12m, coll. AIMS Bioactivity Group 30.1.89, paratype QM GH5431.

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: The colony forms a 3-dimensional reticulum of hard, rigid, sandy,

TABLE 7. Summary of characters of species of *Aplidium* recorded from Australia

Group A: species with the atrial lip not separated from the opening; and with more than 5 stomach folds

Species	Biogeographic Description[1]	Range anticlockwise around Australia	Stomach folds	Systems: form; number	Stigmata: no. rows;no./row	Posterior abdomen	Colony	Embedded sand	Larvae: no. incubated; median trunk length (mm)	Other
A. altarium	WP,tr	Mackay to Cockburn Sd	25–30	radial;one	9–10;25	short	upright cushions	none	3;1.0	
A. australiense	A,te	Recherche Arch. to Shoreham	16	parallel rows; numerous	15;15	long	stalked	none	1;1.5	
A. geminatum n.sp.	A,te	Gt Australian Bight to Western Port	20–23	parallel rows; 1 to 3	15;10–12	"	"	external only	3;0.95	
A. brevilarvacum	A,te	Cockburn Sd to Gt Australian Bight	10	"	14;10	"	"	throughout	1;0.6	
A. inflorescens n.sp.	A,te	Spencer Gulf to Western Port	20	"	15;14–15	"	"	stalk only	4;0.9	
A. parvum	A,te	Albany to Bass Strait	18	"	12;8	"	"	"	3;0.8	
A. congregatum n.sp.	A,tr	Moreton Bay	12	radial; numerous	11;12	"	upright flat-topped	throughout	6;0.5	
A. rosarium n.sp.	A,tr	Capricorn Gp	20	"	12;12	short	cushion	basally	3;0.6	
A. elatum	A,te	Gt Australian Bight	15	branching; numerous	8;8	"	upright lamellae	throughout	?;?	
A. multiplicatum	WP,tr,te	Cockburn Sd to far northern Gt Barrier Reef	22	"	9–11;14–20	"	sheet-like to irregular fleshy mass	none	2–7;0.9	surface even
A. opacum	A,te	Cockburn Sd to Western Port	20	"	12;12	long	"	"	1;0.7	"

[1] A, indigenous; WP, Western Pacific; tr, tropical; te, temperate.

TABLE 7. Summary of characters of species of *Aplidium* recorded from Australia (Group A, Cont.)

Species	Biogeographic Description[1]	Range anticlockwise around Australia	Stomach folds	Systems: form; number	Stigmata: no. rows;no./row	Posterior abdomen	Colony	Embedded sand	Larvae: no. incubated; median trunk length (mm)	Other
A. lodix n.sp.	A,te	Spencer Gulf to Western Port	25	circular; numerous	10;numerous	long	sheetlike	none	6;0.7	surface even
A. robustum n.sp.	A,te	Albany to Tasmania	20	"	14–16;12	"	spherical to conical cushions	"	3;1.06	"
A. multilineatum n.sp.	A,te	Cockburn Sd to Tasmania	30	"	10;16	"	circular cushion	basally	?;0.9	"
A. gastrolineatum n.sp.	A,te	Gt Australian Bight to Pearson I.	24	"	16;14	"	"	external only	?;0.8	ridges surround systems
A. gelasinum n.sp.	A,tr	Northern Great Barrier Reef	16–18	"		16;8	"	"	none	?;? "
A. jacksoni	A,te	Port Jackson	12	"	12;16	"	"	throughout	?;?	surface even
A. ornatum n.sp.	A,tr	SE Qld	25	"	12;10	"	upright flat-topped	none	2;0.7	
A. incubatum n.sp.	A,te	Moreton Bay	25	"	10;15	"	plate to upright flat-topped	throughout	6;0.55	brood pouch
A. uteute	WP,tr	Heron I. to Sarina	25–35	"	11;25	short	sheets	"	2–5;0.7	"
A. fluorescum n.sp.	A,tr	Heron I. to Lizard I.	12–14	"	10;16	"	cushion to sheet-like	"	3;0.5	
A. triggsense	WP,te,tr	Cockburn Sd to Heron I.	15	?	8;10	long	sheets to upright lobes	basally	2;0.6	
A. depressum	WP,tr	Heron I. to Bundaberg	11	?; numerous	5;10	short	sheets	"	3;0.35	no atrial lip
A. minisculum n.sp.	A,te	Vic.	10	circular; numerous	5;10–12	"	cushion to sheets		1;0.4	
A. acroporum n.sp.	A,te	SA	8	"	5;6-7	"	3 dimensional reticulum	throughout	2;0.4	

[1] A, indigenous; WP, Western Pacific; tr, tropical; te, temperate.

TABLE 8. Summary of characters of species of *Aplidium* recorded from Australia

Group B: species with the atrial lip separated from the opening; and usually with 5 stomach folds [1]

Species	Biogeographic Description[2]	Range anticlockwise around Australia	Systems: form; number	Stigmata: no. rows;no./row	Posterior abdomen	Colony	Embedded sand	Larvae: no. incubated; median trunk length(mm)	Other
A. lenticulum n.sp.	A,te	Cockburn Sd to Heron I.	long curved; numerous	16–20;8	long	thick sheets	throughout	1;0.85	systems surround elevated mounds
A. caelestis	WP,tr,te	Shark Bay to Lizard I.	long straight; numerous	10–18;6–14	"	"	"	1;0.65	ridges separate systems
A. rubricollum	A,te	Gt Australian Bight to Western Port	radial; numerous	11–12;14	"	"		1;0.7	ridges surround systems
A. clivosum n.sp.	A,tr,te	Port Hedland to Heron I.	radial; few to numerous	16–18;12	"	massive wedge or thick cushions	"	1;1.75	"
A. crateriferum	WP,tr	Heron I. to Exmouth Gulf	circular; numerous	18–21;14	"	"	"	1;2.0	"
A. lunacratum nom. nov.	A,te	Cervantes to Manning River NSW	circular; numerous	10–15;12–15	"	"	"	1;2.2	"
A. directum	A,te	Cronulla to Moreton Bay	circular; one per lobe	10–13;14	"	upright lobed	"	2;0.55	
A. coniferum	A,te	Elliston Bay to Twofold Bay numerous	circular to radial;	22;8	"	upright stalked	"	1;0.65	surface even
A. magnilarvum n.sp.	A,te	Gt Australian Bight	?; numerous	21;20	"	"	"	1;2.2	"
A. griseum n.sp.	A,tr	Capricorn Group	circular to radial; 2 or 3 per lobe	13;6	"	upright	"	1;0.85	ridges surround systems

[1] the exception is *A. griseum* n.sp. with 8 or 9 stomach folds. [2] A, indigenous; WP, western Pacific; Te, temperate; tr, tropical.

TABLE 9. Summary of characters of species of *Aplidium* recorded from Australia

Group C: species with the atrial lip not separated from the aperture; and usually with 5 stomach folds[1]

Species	Biogeographic Range[2]	Range anticlockwise around Australia	Systems: form; number	Stigmata: no. rows;no.\row	Posterior abdomen	Colony	Embedded sand	Larvae: no. incubated; median trunk length (mm)	Other
A. distaplium n.sp.	A,te	Spencer Gulf to Bass Strait	?; numerous	4;12	short	irregular	throughout	4;0.52	rows of stigmata paired
A. filiforme n.sp.	A,tr	Capricorn Group	circular; 4 or 5 per lobe	5;6	"	upright flat-topped	"	3;0.3–0.47	
A. bacculum n.sp.	A,te	SA	circular; one per lobe	5;6	long	stalked	"	?;?	
A. petrosum n.sp.	A,te	SA	curved; numerous	9;6	"	3-dimensional reticulum	"	3;0.8	
A. solidum n.sp.	A,tr,te	Jervis Bay to Bundaberg and Dampier Arch.	"	9–12;6	short	upright lamellae	"	2–5;0.45	
A. tabascum n.sp.	A,tr	Capricorn Gp, Cockburn Sd	"	15;8	"	sheets or cushions	patchy	2;0.7	
A. ritteri	WP,tr	Heron I.	long; numerous	11–12;7	"	"	"	3;0.55	
A. macrolobatum n.sp.	A,tr	Heron I. to Lizard I.	circular to long; numerous	9–10;15	"	"	"	7;0.65	large lips on aperture
A. paralineatum. n.sp	A,te	Tasmania	long, parallel; 2 or 3	18;12	long	irregular	throughout	?;?	
A. protectans	WP,tr	NSW to far northern Gt Barrier Reef	circular; numerous	18–24;20	"	spheres or domes	none	3;0.85	8 branchial lobes
A. amorphatum	A,te	Elliston Bay to Jervis Bay	"	15;16	"	"	"	1;1.2	8 branchial lobes; parastigmatic vessels
A. parastigmaticum n.sp	A,tr	Heron I.	"	18;12	"	"	"	?;?	parastigmatic vessels

[1] The exception is *A. amorphatum* with 4 stomach folds. [2] A, indigenous; WP, western Pacific; te, temperate; tr, tropical.

branching, anastomosing stalks, usually with horizontal terminal branches that lie in the one horizontal plane. The whole upper surface and the sides of each terminal branch are covered with naked, saucer-shaped circular concavities of 2 to 3 mm diameter, separated from one another by raised sandy ridges. The base of each of these concavities consists of a thin layer of test overlying a shallow thoracic cloacal cavity with a central, sessile cloacal aperture. In the paratype colony (QM GH5431) some of the branches of the stalks, including the terminal ones, are often flattened vertical lamellae.

Zooids are in circular systems of about 10 around each cloacal cavity. Owing to the depressed, transparent, clear, naked test over each cloacal cavity the surface depressions appear deeper than actually they are. Sand is crowded throughout the remainder of the colony. The zooids, smaller than the sand grains, are embedded in the test between the crowded sand grains. Rigid open compartments in the test, which occur in

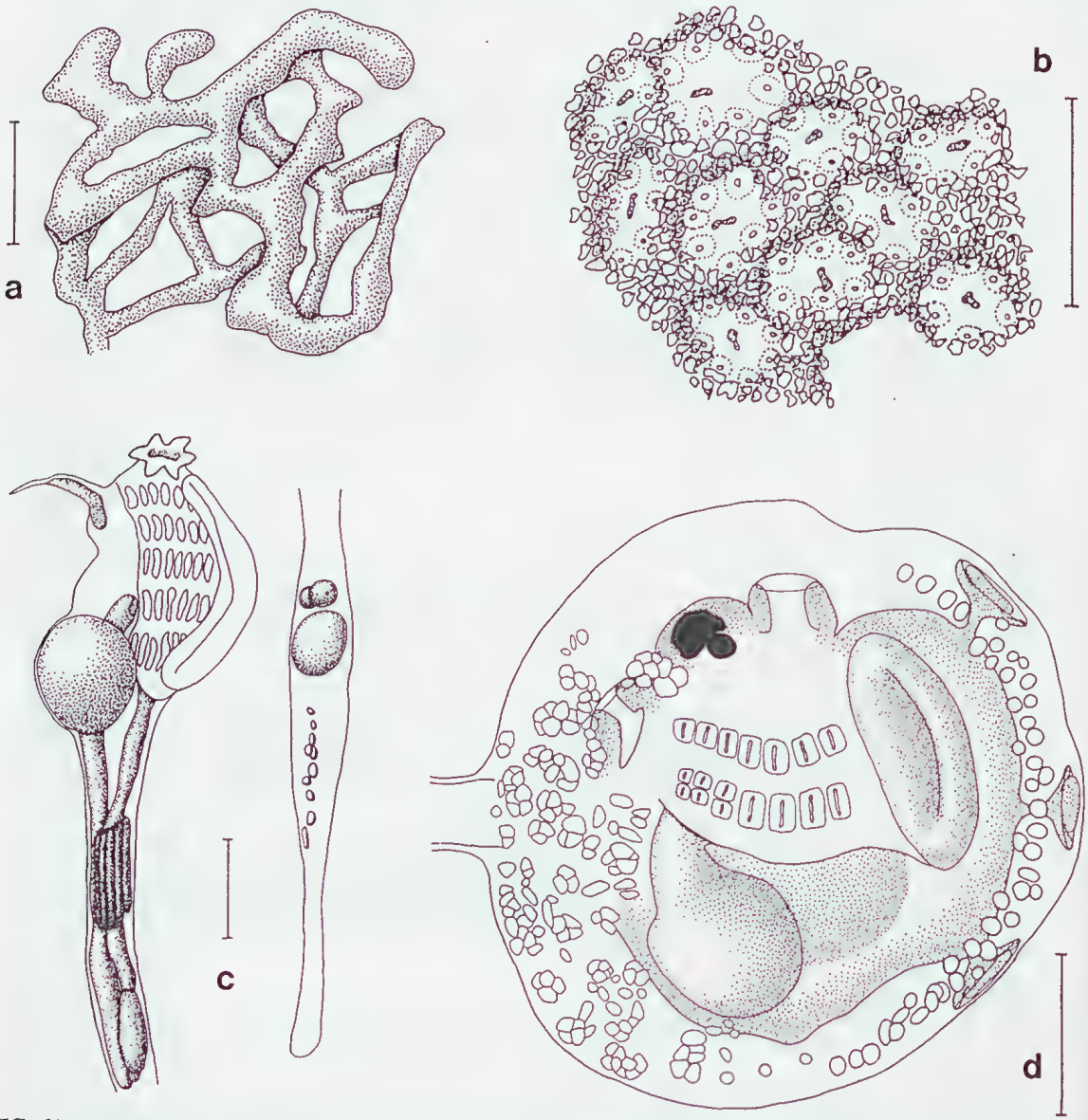


FIG. 61. *Aplidium acroporum* n.sp. — **a**, part of colony (paratype QM GH5443); **b**, surface of colony showing naked areas over cloacal cavities with branchial apertures around the margins (holotype QM GH4169); **c**, zooid, with embryo in atrial cavity and posterior abdomen separately (paratype QM GH5443); **d**, larval trunk, with large test cells (?) posteriorly (QM GH5341). Scales: **a**, 1cm; **b**, 5mm; **c**, 0.2mm; **d**, 0.1mm.

some aplousobranch species to accommodate the zooids, do not occur in the present species.

The maximum dimension of the available specimens is about 10cm and they are 5cm high. However, in no case was the entire colony taken, and it is probable that they are particularly extensive *in situ*. The branches toward the top of the colony have a diameter of 5mm, but the lower branches are narrower, and the basal vertical stalks taper like roots.

INTERNAL STRUCTURE: The zooids are particularly small, up to 2mm long, and thread like. The thorax, abdomen and posterior abdomen are of about equal length, except in those species in which the latter is contracted. The branchial and atrial siphons are short, the former with 6 (sometimes bifid) lobes, and the latter with a single pointed lip from the upper rim of the opening. There are 5 rows of stigmata with 6 or 7 in a row. The small stomach has 8 folds. A short posterior abdomen has 4 or 5 male follicles bunched in it in specimens collected in May. One colony (QM GH5431) collected in February has mature ova in the short posterior abdomen, and 2 embryos are incubated, one at the top of the abdomen and another completely obliterating the atrial cavity.

The larval trunk is spherical, 0.4 mm in diameter, and the tail is wound three-quarters of the way around it. There is a large cerebral vesicle with otolith and ocellus. Epidermal vesicles are in a band about 3 vesicles deep to form a conspicuous arc on each side around the anterior half of the trunk. These develop from a circle of epidermis around the adhesive organs, subsequently becoming detached and scattered in the test. Large morula corpuscles are scattered in the test over each side of the posterior half of the trunk. The 3 adhesive organs are wide but shallow, with short stalks.

REMARKS

Characteristics of the present species are the small zooids and the form of the colony, with its rigid, narrow, sandy branching stalks, and surface depressions separated by raised ridges which give the colony the appearance of the corallites of an acroporid coral.

The anastomosing horizontal terminal branches of this species, with zooid systems opening on the sides and upper surface, probably form a mat above the sandy substrate, with the rest of the reticulum (which lacks zooid openings), buried in the substrate. Such a growth form ensures that the colony is firmly anchored, and must add considerably to the consolidation and stability of the substrate.

The cloacal systems are smaller than similarly shaped ones of *A. lunacratum* nom. nov., from which the species is further distinguished by its 8 (rather than 5) stomach folds, 5 (rather than 9 or more) rows of stigmata and the atrial lip which is separate from the aperture in *A. lunacratum*.

Aplidium altarium (Sluiter, 1909)
(Fig. 62. Plate 10c,d)

Amaroucium altarium Sluiter, 1909, p.105.
Aplidium altarium: ?Millar, 1963, p.695. Kott 1966, p.282. **Not** Michaelsen 1919, p.90. **Not** Millar, 1956, p.914.

DISTRIBUTION

NEW RECORDS: Western Australia (Broome, WAM 873.83 *QM GH2118*; Ningaloo Barrier Reef, WAM 1029.83; Houtman's Abrolhos, WAM 79.75 189.75 388.75 763.82 754.83 837.83 1030.83 *QM GH2146* QM GH5557; Shark Bay, WAM 871–2.83 QM *GH2148 GH2147* 1026–8.83 209.88; Cockburn Sound, WAM 75.75 143.75). Queensland (Moreton Bay, QM GH5478–9; Capricorn Group, QM GH5307 GH5521–2 GH5558–9; Broadhurst Reef QM GH5131; Sarina, QM G4990; Lizard I., QM GH330–1 GH5480).

PREVIOUSLY RECORDED: Western Australia (?Cape Boileau — Millar 1963). Northern Territory (Darwin — AM Y1396 Kott 1966). Indonesia (Sluiter, 1909).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are circular to oval cushions up to 3cm in greatest dimension, lightly attached to hard substrates such as coral skeletons as well as weed. In life the colonies are less flattened, sometimes almost spherical or top-shaped, narrowing basally. They are found either in large populations, their margins probably in contact, to form a mosaic-like covering over the substrate; or they are bunched together. In preservative most of the colonies from Western Australia collected in 1974 to 1979 are a purple colour. Apparently the colour is progressively lost when in preservative for longer, as some from the Abrolhos collected in 1963 (WAM 754-82) are beige transparent cushions. The colour of living colonies is recorded for only one of the Western Australian specimen lots (AMP1 60 QM GH5307), which is said to have been purple and white, although photographs of it are white. It is possible that the colour notes were taken after the specimen was collected, when some oxidation

had taken place. Living colonies from the Capricorn Group were described as 'brick' coloured with white in longitudinal lines down the sides of the colony, or 'pansy purple' (Ridgeway 1886) with beige or yellowish zooids, or 'brown ball ascidians'. The white lines referred to appear to have been calcareous faecal pellets in the cloacal canals. The specimens from Lizard I. and Myora are reported to have been 'maize yellow' (Ridgeway 1886) with a red dot each side of the apertures.

When present, the purple or brick pigment particles are crowded in the surface layer of the soft but turgid gelatinous test of the preserved colonies, becoming more sparse below the surface, and absent altogether from the basal test. Between the pigment particles, and after the pigment has faded, the test is clear and transparent. Sand is neither attached to, nor embedded in, the colony.

Usually a single, central, large, sessile and irregular common cloacal aperture is on the upper surface, and branching cloacal canals converge to it from the outer margin or the base of the upright colonies. Some colonies have up to 3 systems. Zooids, cream in preservative, are arranged in rows along each side of the cloacal canals. They are tightly enclosed in the firm test and are difficult to remove. Their large, white, atrial lips can be seen stretched out along the roof of the cloacal canals, and inserted around the rim of the cloacal apertures. White opaque vesicles in the surface test around the sides and upper surface are terminal ampullae of test vessels.

INTERNAL STRUCTURE: The zooids are about 6mm long when contracted, the thorax, abdomen and posterior abdomen each being about one-third of the total length. About 20 fine longitudinal muscles extend from the thorax along the

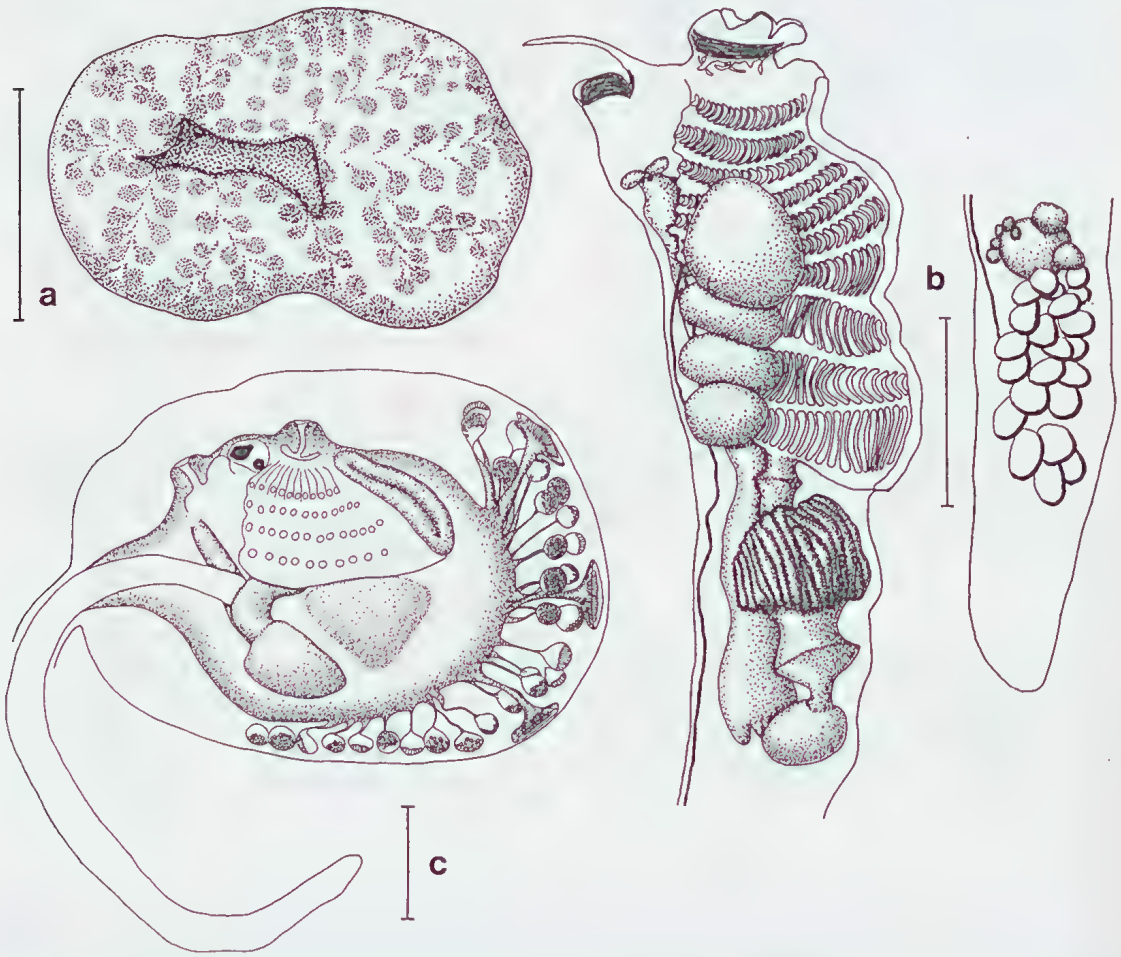


FIG. 62. *Aplidium altarium* — **a**, colony (QM GH5307); **b**, zooid, with posterior abdomen separately (AM Y1396); **c**, larva (WAM 79.75). Scales: **a**, 1cm; **b**, 1mm; **c**, 0.2mm.

length of the zooid, and even though all of the examined zooids are contracted, the muscles are inconspicuous. The branchial siphon is short. Only a short imperforate area is posterior to the prepharyngeal groove. The atrial tongue is of variable length, and is undivided or sometimes divided into 2 or 3 points. It arises from the anterior rim of the atrial aperture. The atrial aperture is a vertical slit, bounded on each side by a projecting convex lip which has muscles in its outer, convex, vertical margin. The homology of these muscles appears to be with the sphincter muscle usually found around the atrial aperture. The unusual configuration of the atrial sphincter in this species results from its component muscle bundle being drawn together by fine longitudinal muscles, one each in the middle of the anterior and posterior rims of the aperture, to form, respectively, the anterior and posterior extremities of a vertical aperture.

As well as being long, the branchial sac is wide, with up to 25 stigmata per row. However, despite its length, there are only 9 or 10 rows of stigmata. The stigmata are long. In the contracted, preserved zooids they usually are found folded horizontally along the centre of each row. The stigmata are fusiform, pointed at each end. They are only slightly reduced in length toward the dorsal and ventral mid-lines.

The oesophagus increases in diameter anterior to the stomach to form a prestomach. The stomach is wide, reduced in diameter at the cardiac end, with some oblique folds terminating against the suture line. It has 25 to 30 fine folds, sometimes interrupted along their length. The duodenum is wide, and the short mid-intestine narrows abruptly to enter the oval posterior stomach in the bend of the gut loop. Short rectal caeca are present at the proximal end of the ascending loop. The rectum extends half way up the branchial sac (opposite the fifth row of stigmata), but the contraction of the anterior part of the thorax can draw the anus up behind the atrial aperture. The anal opening is bounded by two large semicircular lips. The ovary is in the relatively short, stumpy posterior abdomen a short distance behind the gut loop, and 12 to 20 male follicles are clustered behind it. There is no constriction between the abdomen and the posterior abdomen.

Up to 2 embryos are in a brood pouch projecting from the postero-dorsal corner of the thorax in colonies collected in April and May from Western Australia (WAM 754.82 763.82 837.83 1030.83 871–2.83), and from the Capricorn Group in November (QM GH5307) and December (QM GH5559). Mature gonads are not present in colonies collected in August (WAM 1029.83). In the Darwin colonies, collected in October, up to 4 embryos are lined up in the atrial cavity, the largest a tailed larva. Specimens collected in October (QM GH5131) and November (Heron I.), May (Myora) and June (Lizard I.) have up to 3 embryos at various stages crowded into the atrial cavity, projecting dorsally from it when the thorax is contracted. These embryos distend the whole atrial cavity and are not in a postero-dorsal brood pouch as they are when only one embryo is present. Larvae are short and deep, with a trunk to 1mm long. As they mature they become almost spherical, the trunk about 1.0mm long with the tail wound about three-quarters of the way around it. Circles of 6 to 8 epidermal vesicles are around each of the adhesive organs and these remain attached by narrow stalks to the epidermis. About 5 epidermal vesicles are also attached to the trunk ectoderm in the median line ventrally, behind the adhesive organs. The 3 median adhesive organs at the anterior end of the trunk are small and shallow. A mass of blue pigment is in the haemocoelic cavity, especially dense in the posterior horns, although these are largely obliterated as the oozooid develops. Mature larvae with a spherical trunk have 4 rows of stigmata, and a relatively short yolk mass beneath the large, upright pharynx, with its vertical endostyle.

Remarks

The branching cloacal canals of these colonies resemble some species of *Polyclinum*. The mosaics formed by the closely spaced colonies resemble those of *Ritterella dispar*, and some species of *Diplosoma* (see Kott 1980). Nevertheless, the zooids are characteristic of *Aplidium*. It is possible that these lightly attached small colonies subdivide, and move to space themselves evenly over the substrate.

The zooid, sometimes with a brood pouch, and with bunched male follicles in a short posterior abdomen and numerous stomach folds, resembles *Aplidium uteute*. However, the latter species has zooids with longer, more barrel-shaped stomachs, arranged in circular systems, and the colonies are larger and more irregular than those of the present species. Further, although larvae of *A. uteute* have arcs of lateral vesicles, they also have median vesicles which do not occur in the present species. *Aplidium multiplicatum* has branching systems and similar larvae to the present species. However, *A. multiplicatum* colonies are larger, softer, the pigmentation is different, thoraces are nar-

rower and systems longer and more crowded. *Aplidium opacum* has more crowded systems, spreading colonies, narrower thoraces, more rows of stigmata and fewer stomach folds.

A. flavolineatum: Monniot (1987) from Chesterfield Reef has 12 rows of stigmata and about 30 stomach folds. Although Monniot does not record the number of stigmata per row the zooids are similar to the present species. However the colonies are sheet-like rather than being cushions or wedge-shaped lobes, the zooids are arranged in circles rather than radiating double rows, embryos are incubated in a brood pouch and larvae have median ampullae (like *A. uteute*, see below). Although the larvae have some similarities, the present species is not conspecific with the South African *A. flavolineatum* (see Millar 1962) which is sandy (rather than naked) and red (rather than a cream, yellow, purple or brown colour).

The most conspicuous feature of the present colonies, viz. the double-rows of zooids converging to the central or terminal cloacal apertures, were not observed either by Sluiter (1909) or Millar (1963) in specimens they assigned to *Aplidium altarium*. However, the shape of the colonies, the form of the stomach, and the short posterior abdomen without a constriction between it and the abdomen are similar in all descriptions. The large semicircular lips of the anal opening, and its unusual, relatively anterior, position are recorded by Sluiter for the type specimens, which also have an expansion in the oesophagus as in the present specimens. The 4 to 6 embryos reported to be in the atrial cavity (Sluiter 1909, Taf. V9a) are very much smaller than those in the newly recorded specimen — indeed they are smaller than is known for any species of *Aplidium* and possibly Sluiter misinterpreted these bodies. A further discrepancy between Sluiter's account of the type and the newly recorded specimens is that he recorded only 10 stigmata per row — however there often are discrepancies of this order in Sluiter's counts of stigmata.

Reexamination of specimens from Darwin (Kott 1966) shows that the number of stigmata per row and the shape of the colonies were recorded incorrectly. The colonies are cushions, rather than sheet-like and the branchial sacs have the same number of stigmata as the present newly recorded ones. These Darwin colonies appear to be conspecific with the newly recorded specimens and with the Indonesian type material (Sluiter 1909).

Specimens assigned to *A. altarium* from Zanzibar and Mozambique (Michaelsen 1919; Millar 1956) appear different from the present species, with more numerous stomach folds (about 40), and small larvae with only 4 large epidermal vesicles and no ampullae (see Millar 1956).

Aplidium amorphatum Kott, 1963
(Fig. 63)

Aplidium amorphatum Kott, 1963, p.101; 1975, p.6.
Aplidium pseudobesum Kott, 1963, p.101.

DISTRIBUTION

NEW RECORDS: Victoria (Deal I., QM GH ; South Gabo I., QM GH5155–6). New South Wales (Jervis Bay, QM GH5617–9).

PREVIOUSLY RECORDED: South Australia (Elliston Bay — SAM E2581 Kott 1975). Victoria (Bass Strait — AM U3918 Kott 1963). New South Wales (Eden — AM U3922 U3924 Kott 1963).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are soft, gelatinous cushions, about 8cm in diameter, almost spherical or dome-shaped. The test is translucent and the zooids can be seen through it arranged in circular systems of 9 or 10 in each circle, although in these preserved colonies they are generally withdrawn from the surface and the systems are obscured. Specimens from South Gabo I. (QM GH5155–6) are described by the collector as 'red rose' ascidians.

INTERNAL STRUCTURE: The zooids are large, the thorax and abdomen together being about 5mm long. In relaxed condition the thorax would be longer than the abdomen. The posterior abdomen is long, but when contracted is drawn up to the left side of the gut loop. The zooids are muscular with about 20 longitudinal bands on the thorax that extend along the ventral border of the abdomen and posterior abdomen. The branchial aperture has 8 pointed to shallow rounded lobes around the rim of the short siphon. The long, robust, tongue-like atrial lip, from the upper border of the opening, has a tridentate tip with each division of equal size. The pharynx has 15 rows of up to 16 long stigmata. Each of the rows is crossed by a parastigmatic vessel. An intermediate dorsal languet associated with each of these parastigmatic vessels alternates with, and is the same size as, the languets on the primary transverse vessels.

The oesophagus is about one third of the length of the abdomen. The large voluminous stomach occupies the middle third. It has 4 shallow glandular ridges in its internal wall. The usual duodenal and mid-intestinal regions and a pear-shaped posterior stomach are in the posterior third of the descending limb of the gut loop. A double series of testis follicles is in the posterior end of the posterior abdomen and the ovary is anterior to them.

The colony from Elliston Bay collected in February has a single, large, embryo being incubated in the atrial cavity, almost completely occluding the pharynx. The larval trunk is 1.2mm long, and the tail is wound only halfway around it. Ectodermal vesicles are crowded in the test around the anterior part of the trunk, obscuring the 3 adhesive organs in the anterior mid-line. They consist of wide lateral bands of vesicles, and some in the median line attached by 2 or 3 long branching stalks in each interspace between the adhesive organs. The developing adult organs are at the posterior end of the long trunk.

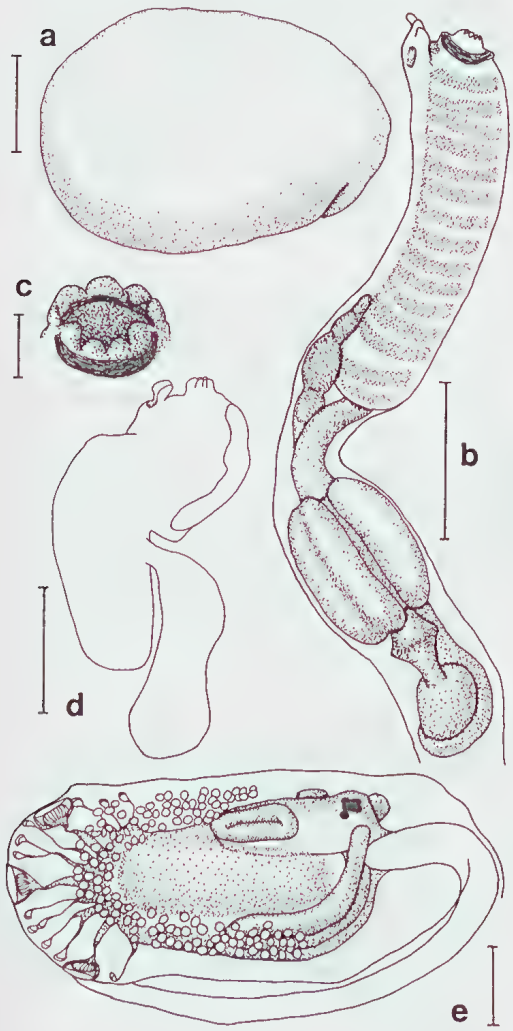


FIG. 63. *Aplidium amorphatum* — **a**, colony outline (SAM E2581); **b**, thorax and abdomen (holotype AM U3918); **c**, branchial aperture (holotype AM U3918); **d**, outline of contracted zooid, showing posterior abdomen pulled up alongside the abdomen (QM GH5617); **e**, larva (SAM E2581). Scales: **a**, 2cm; **b**, 1mm; **c**, **e**, 0.2mm; **d**, 2mm.

REMARKS

The distinctive aspects of this species are its soft, rounded colonies, large zooids in circular systems, 8 branchial lobes, parastigmatic vessels, large stomach with shallow glandular ridges, and the large larva filling the atrial cavity in which it is brooded. The species has a superficial resemblance to *Aplidium protectans* which also completely lacks sand, and has a similar rounded shape, circular systems, 8 branchial lobes, large zooids, and shallow stomach folds. However, in *A. protectans* the test is firmer, the systems are depressed into the surface test, rows of stigmata are more numerous, parastigmatic vessels are absent, and the range is tropical.

The wide ventral muscle which draws the posterior abdomen up alongside the posterior end of the abdomen is reminiscent of the muscle band in *Aplidium circumvolutum* which distorts the zooid in a similar way (see Miller 1982).

Aplidium australiense Kott, 1963
(Fig. 64)

Aplidium australiensis Kott, 1963, p.111 (part, type specimen from Shoreham).
Aplidium colelloides: Kott 1972a, p.15; 1972b, p.176; 1975, p.7.

DISTRIBUTION

NEW RECORDS: Western Australia (Recherche Archipelago, WAM 147.75). South Australia (Eyre Peninsula, SAM E2557; Great Australian Bight, SAM E2478; Nuyts Archipelago, SAM E2472 E2476 E2558; Hotspot, QM GH1325).

PREVIOUSLY RECORDED: South Australia (Great Australian Bight — Kott 1972b, 1975; St. Vincent Gulf — Kott 1972a; Investigator Strait — Kott 1972b). Victoria (Shoreham — AM Y1398 holotype Kott 1963).

The records suggest that the species occurs only off the southern Australian coast.

Description

EXTERNAL APPEARANCE: The colonies are long (up to 8cm), more or less elliptical heads to 6cm diameter on long (to 20cm) narrow, tough, sandy stalks narrowing to a basal holdfast of short, thick root-like branches. The test on the head is soft, gelatinous, translucent. The terminal end of the head sometimes is pointed.

In the larger preserved colonies there are 4 to 6 deep, longitudinal furrows or creases formed between deep folds of the surface of the colony. Common cloacal canals are at mid-thoracic level and extend into large cloacal spaces in the edge of the folds referred to above. Three or 4 large cloacal apertures are either sessile or on protuberant cones along the edge of the folds. Sometimes they seem to alternate from side to side of the edge of the fold. Branchial openings of zooids are on both sides of these folds, i.e. on their outer and inner surfaces, as well as in the base of the depressions between and under the folds. Branchial apertures are absent only from the edges of the folds over the large cloacal canals.

Zooids are seen to be in longitudinal rows near the top of the stalk. However, in preserved colonies the arrangement of zooids towards the middle and top of the head is obscure.

Relatively small heads (2cm long) on long (10cm) stalks (SAM E2558) suggest that heads may regenerate on persisting stalks. These smaller heads lack the deep creases of the larger ones, and the zooids are arranged in more or less conspicuous double rows, converging to large cloacal apertures — 3 or 4 randomly distributed around the sides of the head, and 2 or 3 on the top of the head.

INTERNAL STRUCTURE: Zooids are particularly long and thread-like, their posterior ends curving down into the stalk. The rim of the branchial apertures is divided into 6 large, rounded lobes. The atrial aperture is a small sessile opening in the middle of the dorsal border of the thorax with a small pointed languet from the upper rim of the opening. About 10 longitudinal muscle bands on the thorax extend the length of the zooid, joining into a single wide ventral band along the long posterior abdomen.

Stigmata are in 15 rows with about 15 per row, although both the number of rows and the number per row are difficult to count owing to contraction of the small zooids. Twelve to 16 deep, longitudinal folds are in the stomach wall. The number varies with the size of the zooids. Testis follicles are in a double series in the posterior end of the posterior abdomen.

One large embryo or tailed larva and sometimes also what appears to be an infertile ovum are in the posterior part of the atrial cavity in colonies collected in September (SAM E2557) and in October (Kott 1972b). Specimens collected in March (SAM E2476) have mature male gonads.

The larval trunk is 1.5mm long. Its anterior end is obscured by a cloud of minute epidermal vesicles along each side of the base of the adhesive organs. The tail is wound three-quarters of the way around the trunk.

Remarks

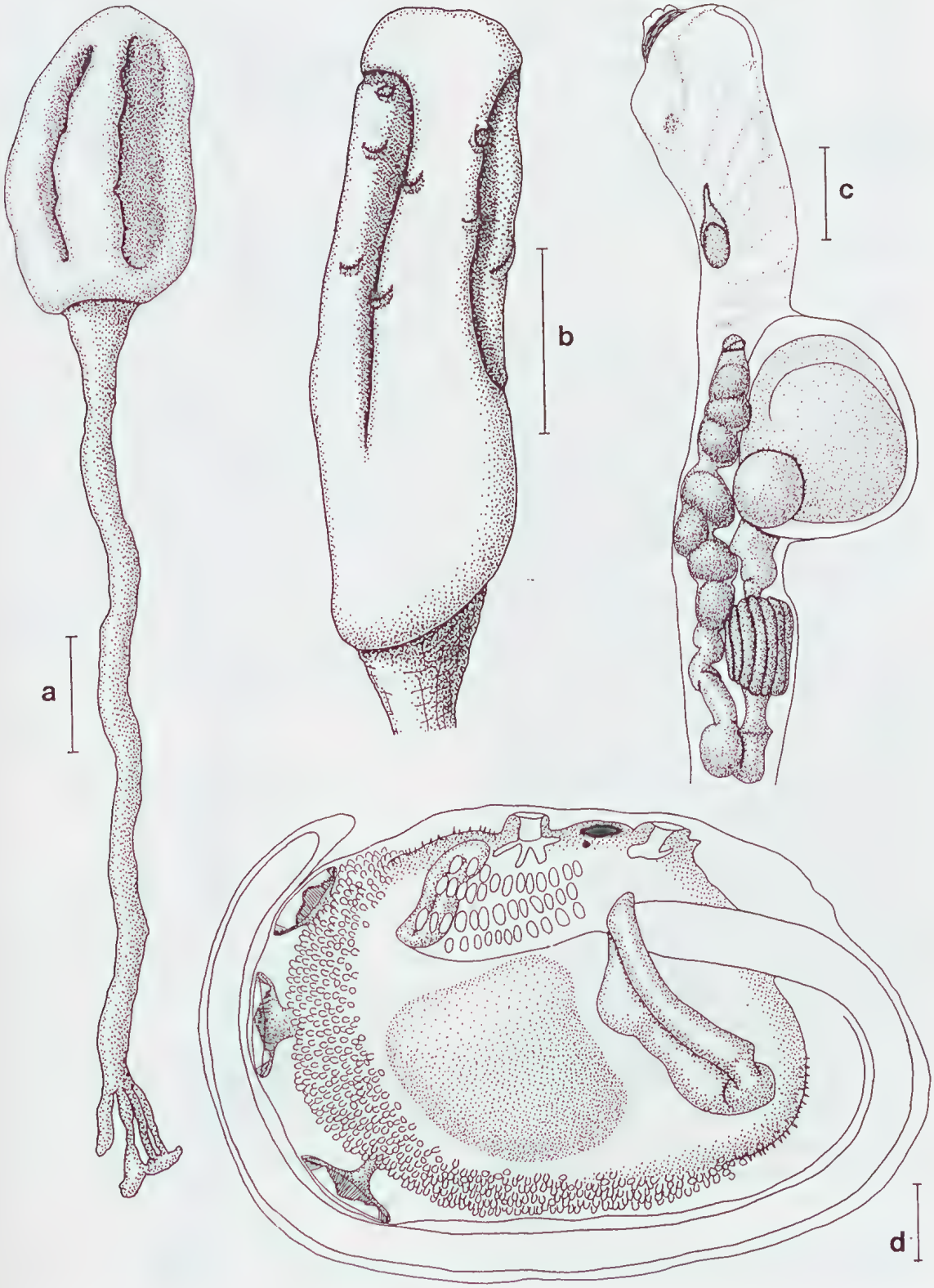
The colonies of this species, with their long, narrow, hard, sandy stalks and long gelatinous heads with small, crowded zooids and deep longitudinal creases, are distinctive.

Despite Herdman's (1886) speculation that *Aplidium colelloides* (Herdman, 1886) from South Africa had a short stalk, Millar (1962) established that it has a long (up to 6cm), narrow, hard stalk like that of the present species and reminiscent also of the long-stalks of species of *Sycozoa* and *Pseudodistoma*. Kott (1972a,b; 1975) in assigning South Australian specimens to the South African species, ignored the fact that the former have larger colonies with external creases on the head, more numerous stomach folds, and a larval trunk twice the size of the South African specimens. The large colonies that characterise the Australian species also have more crowded zooids less conspicuously arranged in long, oval systems (Millar 1962).

The larger colonies, deep creases, complex crowded systems as well as the long, narrow, hard stalks help to distinguish the species from *A. geminatum* n.sp. which has double rows of zooids, but short and thick stalks, less crowded zooids, more numerous stomach folds, longer, more conspicuous and often 3-lobed atrial tongues, and different larvae.

The type specimen of the present species from Shoreham (AM Y1398) is a head which has lost its stalk. The other specimens assigned to this species by Kott (1963) are colonies of

FIG. 64. *Aplidium australiense* — **a**, whole colony (QM GH1325); **b**, head of large colony (SAM E2478); **c**, thorax and abdomen with embryos being brooded in posterior end of atrial cavity (SAM E2557); **d**, larva (SAM E2557). Scales: **a**, **b**, 2cm; **c**, 0.5mm; **d**, 0.2mm.


a
b
c
d

A. geminatum n.sp., to which the larva figured by Kott (1963, Fig. 25) also belongs.

Aplidium bacculum n.sp.
(Fig. 65. Plate 10e)

DISTRIBUTION
TYPE LOCALITY: South Australia (Yorke Peninsula, Edithburgh, 35°9.7S 137°47.4E, 12m, coll. AIMS Bioactivity Group 6.2.89, holotype QM GH 5434).
FURTHER RECORD: South Australia (Thorny Passage, SAM E2568).

DESCRIPTION
EXTERNAL APPEARANCE: The colony is a compact mass of parallel, long (3cm), narrow (to 5mm) sandy stalks, that branch once or twice along their length and adhere to one another. Their terminal free ends are flattened, horizontal, and level with one another to form a more or less even platform. They have a cloacal aperture in the centre of each terminal flat tip. This opens from a shallow, circular, cloacal cavity which is surrounded by about 10 zooids. Branchial apertures open around the upper margin of the terminal flat surface, and atrial apertures open into the cloacal cavity. A single cloacal system is in each terminal branch. The specimens from Thorny Passage have the terminal test inflated over each zooid, and the central common cloacal apertures protrude slightly.

Sand is crowded over the surface of each stalk, and also is embedded throughout the internal test, but is absent from the surface over the terminal end of each lobe. The small thread-like zooids are difficult to remove from their narrow longitudinal spaces in the hard, sandy colony.

INTERNAL STRUCTURE: Zooids extend the whole length of the sandy stalk, but the thorax and abdomen are together only about 3mm of which the abdomen is about two-thirds. The branchial aperture has 6 rounded lobes. A fleshy atrial lip, divided into 3 pointed lobes, extends from the upper border of the atrial aperture. Longitudinal muscles on the thorax are moderately strong, but they become finer as they extend back along the ventral surface of abdomen and posterior abdomen in a wide band of delicate muscles.

Stigmata are in 5 rows of about 6 stigmata per row, but these were difficult to count owing to contraction. The oesophagus is relatively long,

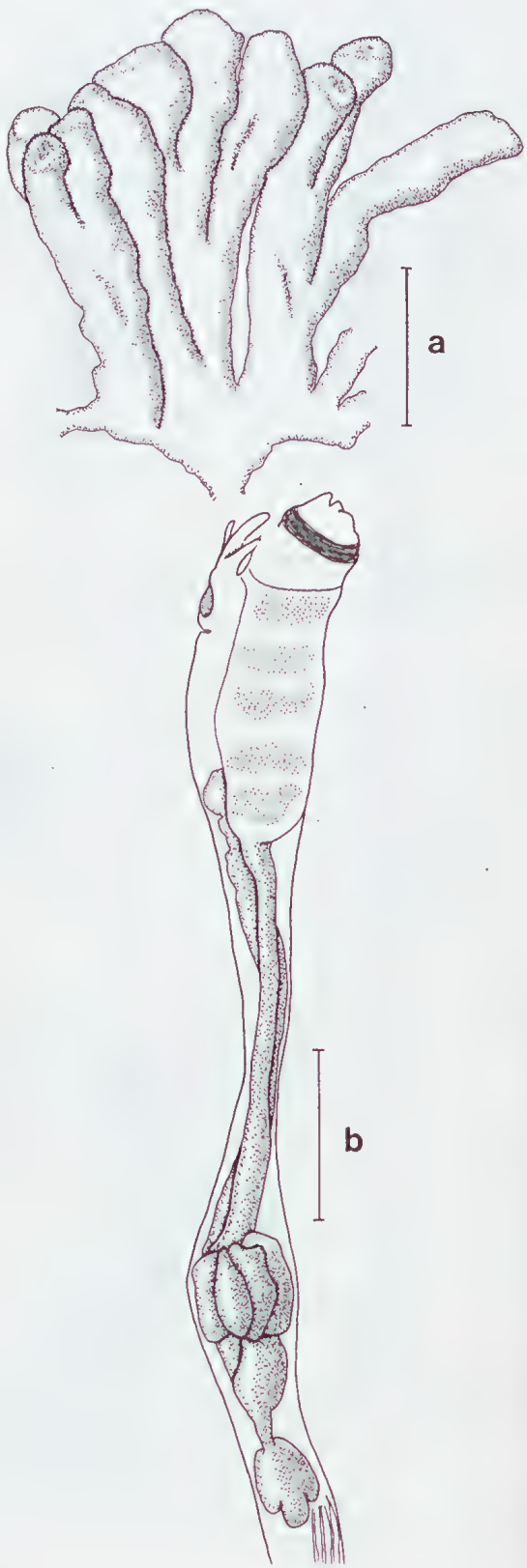


FIG. 65. *Aplidium bacculum* n.sp. (holotype QM GH5434) — **a**, colony; **b**, thorax and abdomen. Scales: **a**, 1cm; **b**, 0.5mm.

the small stomach being two-thirds of the way down the abdomen. The stomach wall has 5 deep folds. The duodenal area reduces in diameter to a short mid-intestine which opens into an oval posterior stomach in the descending limb of the gut loop. There is a small rectal valve at the proximal end of the rectum. Gonads are not developed in the available material.

REMARKS

Superficially, the sandy stalks of this species differ from those of *Ritterella* spp. and *Monniotus* spp. (which have no sand internally) principally in having embedded sand crowded in the internal test. Despite the long oesophagus, however, zooids are characteristic of *Aplidium* and open into a well developed cloacal cavity rather than directly to the exterior as in *Ritterella*. The form of the colony, and the long oesophagus (which probably is associated with the length of the colony lobes), together with the small zooids with only 5 rows of stigmata, characterise the species. Externally, the sandy lobes of the colony, especially the one from Thorny Passage with the test inflated over the anterior end of each zooid, and the protruding central cloacal aperture, resemble *Synoicum stewartense* Michaelsen, 1924 (see Millar 1982).

Other *Aplidium* species with 5 rows of stigmata viz. *A. filiforme* n.sp. and *A. depressum* lack the long stalks and long oesophagus of the present species.

Aplidium brevilarvacium Kott, 1963
(Fig. 66. Plate 10f,g)

Aplidium brevilarvacium Kott, 1963, p.113.
Aplidium digitatum Kott, 1975, p.7.

DISTRIBUTION

NEW RECORDS: South Australia (Ward I., QM GH2412; Top Gallant I., QM GH953; Investigator Group, QM GH1311 GH2413). Queensland (Heron I., QM GH961).

PREVIOUSLY RECORDED: Western Australia (Pt. Peron; Cape Naturaliste — AM U3926 syntypes *A. brevilarvacium* Kott, 1963). South Australia (Northern Great Australian Bight – QM G7508 AM Y1982 paratypes *A. digitatum* Kott, 1975).

The record from Heron I. is anomalous (see Remarks, below).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are rounded heads (0.5 to 1.5cm in diameter) on thick stalks, 0.5 to 6.0cm long, branching 2 or 3 times along their length, and up to about 0.5cm in diameter at the base. These sometimes arise from a basal test mass. Zooids are arranged in longitudinal rows along each side of cloacal canals that extend the length of the head, converging to 2 or 3 large, terminal cloacal apertures. The outer surface of both head and stalk is even, without wrinkles or protuberances.

There is a layer of sand in the outer surface that may obscure the zooids and their branchial openings. Sand is present also in the internal test. The anterior ends of the zooids are perpendicular to the outer surface and posteriorly they curve down into the stalk of the colony, criss-crossing one another as they go. In life the colonies are white to a sandy pink colour.

INTERNAL STRUCTURE: Zooids are robust. When contracted the thorax and abdomen are of equal length and together about 2mm long. About 12 very fine longitudinal muscles from the thorax run the length of the zooid. The branchial lobes are rounded. The atrial opening is sessile, with a fleshy, pointed lip from the anterior rim of the opening which sometimes is divided into 2 at the tip. The pointed dorsal languets are to the left of the mid-dorsal line, opposite the third row of stigmata. Stigmata are relatively short and oval, about 10 per row, and in 14 rows. The stomach, halfway down the abdomen has 10 deep longitudinal folds. The duodenum is long, and the oval posterior stomach is separated from the duodenum and rectum respectively by short lengths of proximal and distal mid-intestine. The posterior abdomen is narrow, up to 1cm long.

In the type specimens from Cape Naturaliste (collected in January) and the newly recorded South Australian specimens (collected in April) there is a large tailed embryo in the atrial cavity and sometimes a large (possibly non-fertile) ovum as well. The larval trunk is about 0.9mm deep, but only about 0.6mm long. It has an ocellus and an otolith, 3 medium stalked adhesive organs, and the tail is wound one and a half times around it. Epidermal vesicles are present along each side of the adhesive organs.

REMARKS

The colonies from Heron I. appear to have only one or 2 terminal cloacal apertures, instead of the more numerous openings in the South Australian colonies. However the zooids have the same number of rows of stigmata and stomach folds, and are not distinguishable from the southern or western Australian ones. These Heron I. colonies may

represent a population at the northern extremity of the range of this otherwise temperate indigenous species.

Externally, the colonies of this species, and particularly the specimens from Heron I. with one or 2 systems per lobe resemble *Distaplia australiensis* (see Kott 1990). Colonies also resemble *Aplidium geminatum* n.sp. which, however, has more numerous (20), fine stomach folds, appreciably larger colonies, and less branched and more wrinkled stalks.

Aplidium caelestis Monniot, 1987
(Fig. 67. Plate 11a–f)

Aplidium caelestis Monniot, 1987, p.517.
Synoicum hypurgon: Kott, 1963, p.86.
?*Aplidium* aff. *lobatum*: Tokioka, 1967, p.22.

DISTRIBUTION

NEW RECORDS: Western Australia (Shark Bay, WAM 883.83; Mullaloo Beach, QM GH5450; Hillary's Boat Harbour, QM GH5452). South Australia (Edithburgh, QM GH5437; Beachport, SAM E2566 E2569; Kangaroo I., QM GH5428 GH5430). Victoria (Bass Strait QM GH5648). NSW (Norfolk I., QM GH5783). Queensland (Capricorn Group, QM G9474 GH5594 GH5633–40 GH5647–8 GH5650–9 GH5661–2 GH5665; Lizard I., QM GH5631–2).

PREVIOUSLY RECORDED: Western Australia (Rottnest — AM Y1382 Kott 1963). Queensland (Heron I. — AM U3991 Kott 1963). New Caledonia (Monniot, 1987). ? Marianas (Tokioka 1967).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies form robust, always sandy, investing sheets up to 20cm

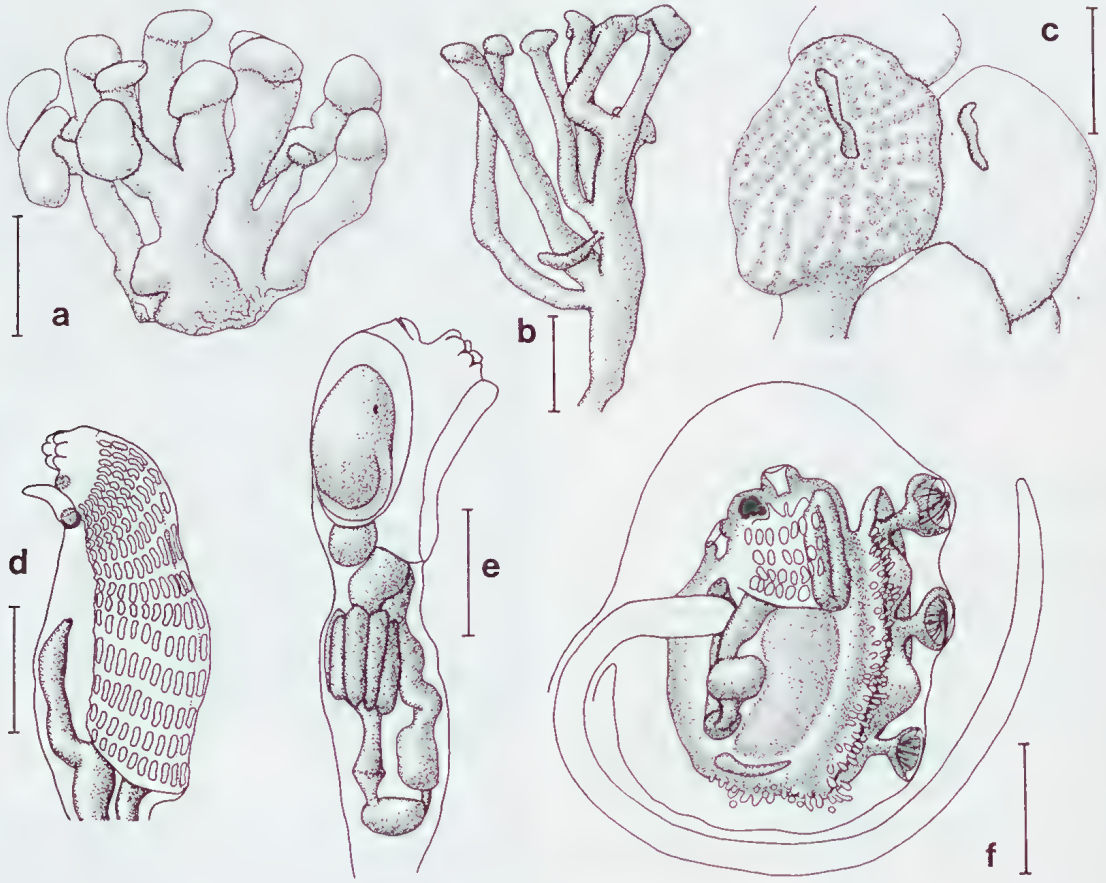


FIG. 66. *Aplidium brevilarvacium* — **a**, **b**, parts of colonies (QM GH953, G7508); **c**, details of a zooid system, with double rows of zooids converging to a terminal cloacal cavity (QM GH961); **d**, thorax (QM GH2412); **e**, thorax and abdomen (QM GH953); **f**, larva, showing arcs of lateral vesicles and median ampullae (syntypes AM U3926). Scales: **a**, **b**, 2cm; **c**, 5mm; **d**, **e**, 0.5mm; **f**, 0.2mm.

in maximum extent and up to 1cm thick. A row of zooids is along each side of the cloacal canals that extend between or around long, narrow areas of zooid-free test. Large sessile common cloacal apertures are at the junction of several canals and they often are elevated by the large cavity beneath them. The surface of the colony is depressed where relatively thin, usually transparent, naked test overlies the cloacal canals. Oval granular bodies about 0.1mm long, and some shade of brown to almost black are in the test and line the sides, base and walls of the cloacal canals, and often are in the surface as well. The grey to brown colour of the colonies results from these bodies and the included sand, sometimes in small clumps. Both the oval bodies and the clumps of sand appear to have been interpreted as faecal pellets. Sand is embedded throughout the test except in the thin transparent surface layer over the cloacal canals. Colonies have been described as 'sandy grey' or 'drab, with fawn zooids', 'sandy grey with yellow zooids', 'grey encrusting ascidian'. Living zooids are yellow, or orange. The test over the cloacal canals is irridescent in

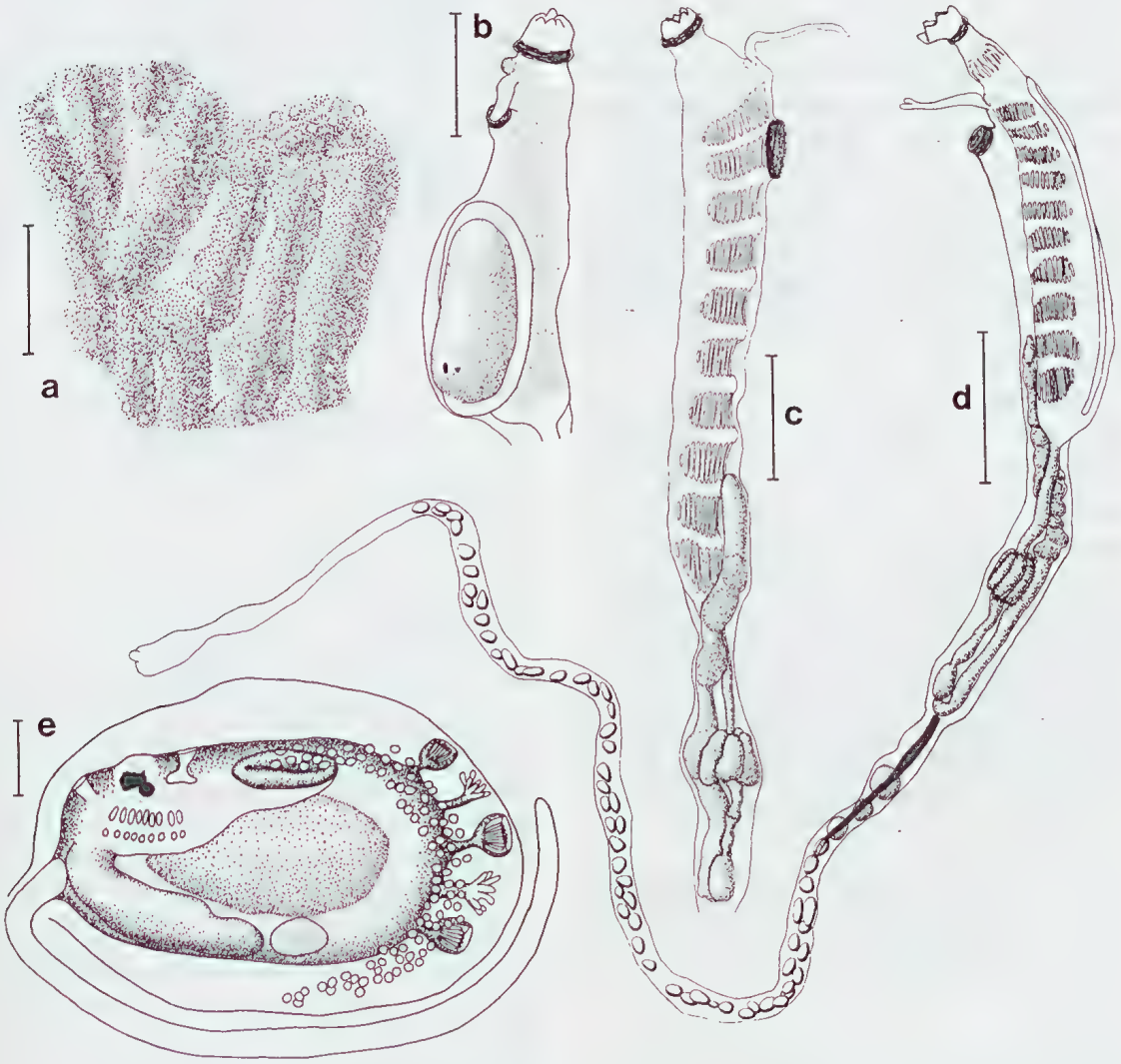


FIG. 67. *Aplidium caelestis* — **a**, colony (QM GH5437); **b**, thorax with embryo being incubated (QM GH5150); **c**, thorax and abdomen (QM GH5647); **d**, whole zooid (QM GH5633); **e**, larva (QM GH5647). Scales: **a**, 5mm; **b**, **c**, 0.5mm; **d**, 1mm; **e**, 0.1mm.

living specimens. A colony from Heron I. (QM GH5661) had blue cells in the surface test between the rows of zooids of the living colony — as in the type from New Caledonia. *Prochloron* is often present on the surface (see Kott *et al.*, 1984: *Aplidium* sp. 1). Two colonies have red and green symbiotic cells embedded amongst the sand in the floor of the common cloacal canals. These are pink in preservative. Sand always is present in the basal half of the colony, and in the ridges between the double rows of zooids.

INTERNAL STRUCTURE: The zooids are long and thin (thorax and abdomen together to 5mm), but robust, with strong longitudinal muscles that extend their full length, along the ventrum of abdomen and posterior abdomen. The thorax and abdomen, of about equal length, are together about 3mm. The branchial siphon has 6 rounded lobes and a single conspicuous bulging sphincter muscle at their base. A long prebranchial area is posterior to the tentacles. The atrial aperture, a short distance down the dorsal surface, also has a conspicuous sphincter muscle. A robust, but not very long, pointed atrial lip, usually not divided, arises from the body wall anterior to the aperture. The atrial aperture at the level of the second or third row of stigmata opens into the sides or base of the cloacal canal.

Stigmata are in 10 to 18 rows, with 6 to 14 the maximum number per row. Expanses of unperforated pharynx are along each side of the mid-dorsal and mid-ventral lines. The oesophagus and post-pyloric part of the gut loop are relatively long for this genus, the gut loop being about the same length as the thorax when both are extended. The small stomach, halfway down the abdomen, has 5 distinct folds, although these sometimes flatten and occasionally it is difficult to see traces of any folds in the stomach wall. The duodenum, mid-intestine and posterior stomach are characteristic of the genus. Gonads are in the centre of the abdomen and consist of an irregular row of testis follicles with an anterior ovary a little distance behind the gut loop.

A single embryo with a trunk 0.65mm long and median ampullae alternating with the adhesive organs is in the atrial cavity of specimens taken in March and August from Heron I.

REMARKS

The zooids of this species, with their well-formed branchial siphons, sphincter muscles, atrial lips separate from the apertures, and long and narrow thoraces, resemble *A. crateriferum*, *A. griseum* n.sp., *A. lenticulum* n.sp., *A. lunacratum* nom. nov. and *A. clivosum* n.sp. The long, rather straight double row systems with long canals surrounding ridges of solid sandy test, sometimes can be seen in *A. ritteri*, but its atrial lip is not separate from the aperture. The oval granular bodies are present also in *A. lenticulum* n.sp., which has cloacal canals around raised polygonal areas rather than between the long ridges of the present species. The larvae also appear to be similar to those of *A. lenticulum* n.sp. The type specimen of *A. caelestis* Monniot, 1987 from New Caledonia has the same almost smooth stomach, narrow thorax, separate atrial lip, long double rows of zooids. The test is entirely encrusted with sand as it usually is in the newly recorded specimens. Although the transparent test over the cloacal canals is not always sky-blue in living specimens as it is in the type, it sometimes is. Colour and the number of rows of stigmata appear to be variable characters in this widespread species.

Kott (1963), interpreting the oval bodies as faecal pellets, assigned specimens of this species to *A. hypurgon* (Michaelsen, 1924), a New Zealand temperate species.

Aplidium clivosum n.sp.
(Fig. 68. Plate 12a–f)

Aplidium pantherinum: Kott, 1963, p. 98; 1972b, p. 176.

DISTRIBUTION

TYPE LOCALITY: South Australia (S.E. Beachport, 6–7m, on jetty piles, coll. W. Zeidler 20.2.89, holotype SAM E2561; Kangaroo I., on jetty piles, coll. N. Coleman 12.3.78 AMPI 220, paratype QM G1197).

FURTHER RECORDS: Western Australia (Port Hedland, WAM 1020-2.83; Montebello Is, QM GH5406; Cockburn Sound WAM 869–70.83, QM GH2149; Busselton, QM GH5469; Green Pools, QM GH5629). South Australia (Topgallant I., QM GH1287 QM GH2419; Hotspot, QM GH2417; Nuyts Archipelago, SAM E2562; Eyre Peninsular, SAM E2566 E2569; Flinders I., QM GH2305; Kangaroo I, QM G11997 GH5432 GH5433, SAM E2564; Ward I., Beachport, QM GH5447; West I., QM GH2415). New South Wales (Jervis Bay AMPI 78 QM GH5628). Queensland (Heron I. QM GH5569 GH5593 GH5597 GH5669–70 GH5675); Western Australia (Rottnest to Hamelin Bay — Kott 1963). South Australia (Elliston Bay — SAM E2585 Kott 1972b).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are large, to 4cm thick and to 15cm or more in maximum dimension. Some are of even thickness attached by the whole of the basal surface. Others converge toward the basal attachment area, or have irregular processes that may project into the substrate or around rocks and rubble. One colony (WAM 1021.83) is upright, rather flattened and divided into 2 lobes, about 15cm high, with systems evenly distributed over the both sides of the upright lobes.

The base and sides of the colonies have sand adhering to the surface. Sand usually is present on the zooid-free raised areas of the surface surrounding single systems, or groups of systems. The test over the systems usually is naked. Embedded sand is absent at thoracic level where zooids curve around the shallow cloacal cavities, but is present throughout the remainder of the test. In some colonies it can be seen projecting in from the periphery of each system as narrow wedges between the double rows of zooids.

The cloacal canals converge from the periphery of each system, to the large central cloacal cavity. A cloacal aperture raised on a conical protuberance (up to 5mm diameter across the base) is in the centre of each system. Zooids are arranged in double rows, one row along each side of the canals. In preserved colonies the surface is depressed over the systems, although it is not unusual for 3 or 4 systems to be present in one large depression, each system with its protruding common cloacal aperture. Systems are not always circular, often being irregularly shaped, the cloacal aperture being excentric with longer canals on one side than on the other. The diameter of the systems in this species is variable, ranging from 0.5 to 1cm, often in one colony.

In some colonies the whole upper surface is horizontal, and depressed within a rounded marginal rim. In others there is no sharp division between the margin and a convex upper surface.

In photographs, living colonies are pink, 'light wine' or bluish red. In preservative they are a translucent bluish-red. The colour is conspicuous on the upper surface over the systems and around the cloacal apertures.

INTERNAL STRUCTURE: In contracted zooids the thorax and abdomen together are from 3 to 6mm long. Long, thread-like posterior abdomina extend down through the crowded sand in the lower half of the colony.

About 12 fine longitudinal thoracic muscles extend posteriorly along the whole length of the zooids. The branchial siphon is long, with a narrow, bulging sphincter muscle behind the branchial lobes. Some fine circular muscles are on the remainder of the siphon, but they do not form a sphincter. The branchial tentacles are about halfway up the branchial siphon, with a long prepharyngeal area between them and the prepharyngeal groove. The diameter of the siphon bulges out in the vicinity of the branchial tentacles between the anterior sphincter and the prepharyngeal groove. A single, pointed atrial lip, sometimes bifid or trifid at the tip, arises from the body wall just anterior to the atrial siphon, which, depending on the state of contraction of its sphincter muscle, is either a sessile, circular opening, or is on a short, cylindrical siphon. The atrial siphon is well anterior, opposite the second row of stigmata.

In the branchial sac are 16 to 18 rows of up to 12 stigmata. A wide unperforated band of pharyngeal wall is present each side of the endostyle.

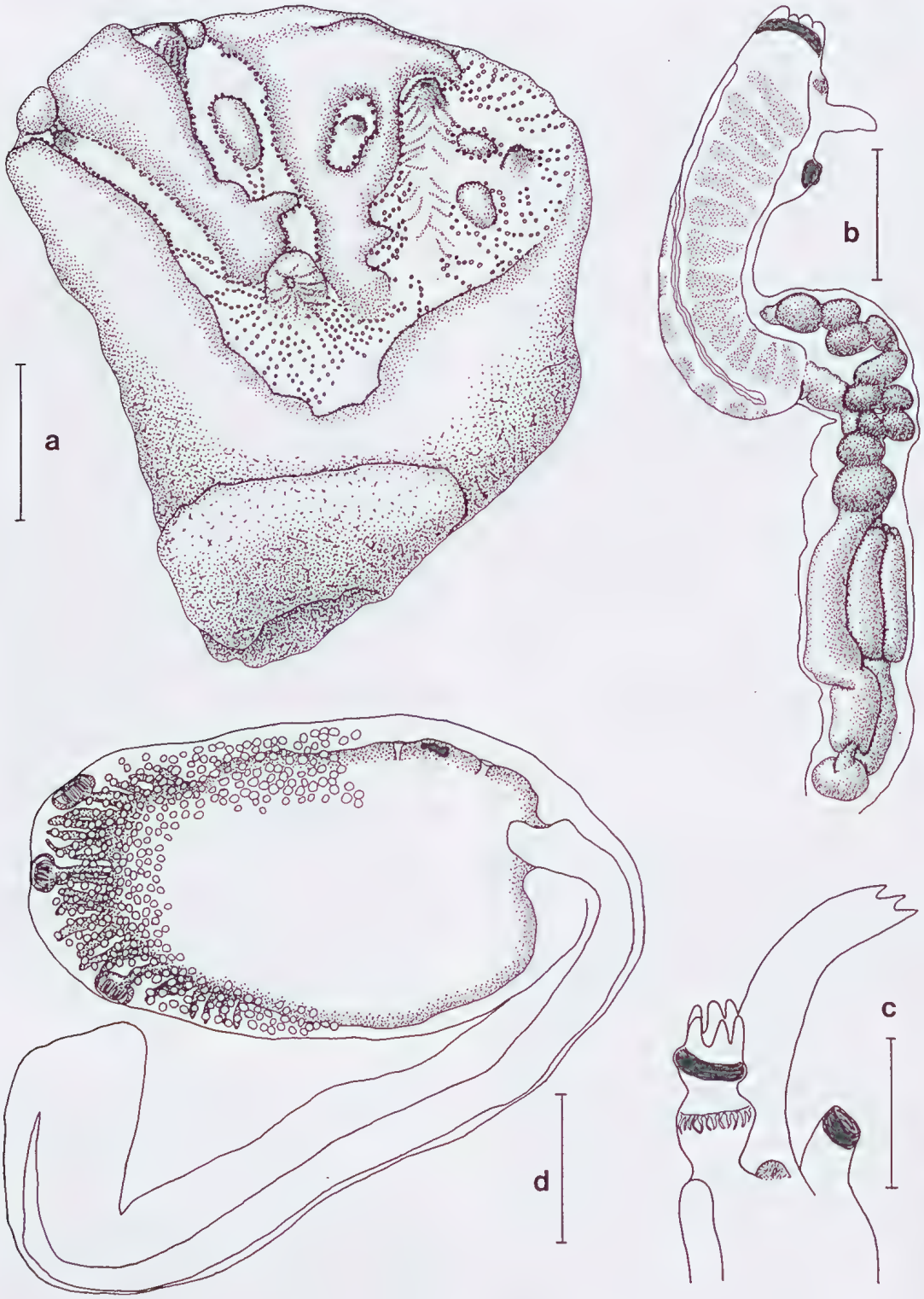
The abdomen is almost as long as the thorax. The oesophagus is long and narrow. The small stomach has 5 deep folds in its wall. A long duodenum is continuous with a narrow proximal part of the mid-intestine. A small oval posterior stomach is in the distal part of the descending limb of the gut loop. A short, narrow distal section of the mid-intestine is between the posterior stomach and rectum in the bend of the gut loop. A distinct rectal valve is present. The anal opening is opposite the fourth most posterior row of stigmata.

A single or double series of male follicles is in the posterior part of the posterior abdomen.

A large embryo (trunk 1.5 to 2.5mm long) is in the posterior half of the atrial cavity of specimens collected in March at Busselton (QM GH5469), and January at Kangaroo I. (QM GH5432). The tail extends only to the anterior end of the trunk which has crowded hair-like ampullae obscuring the anterior end. Embryos and larvae are heavily pigmented (red and opaque).

REMARKS

The species is distinguished by 2 characters which although they occur separately in other species, seldom are found together as they are in the present one — the atrial lip is close to, but separated from the aperture, and the double rows of zooids converge to the cloacal aperture. It also has a group of characters which it shares with *A. crateriferum* and the temperate and partly sympatric *A. lunacratum* nom. nov., viz. the bulky sandy colonies, protuberant cloacal apertures, narrow


a
b
c
d

zooids with 5 well-formed stomach folds, and the atrial lip separate from the aperture.

The zooid systems are not always so deeply depressed into the surface as they are in *A. crateriferum*, and *A. lunacratum* nom. nov. has sand in the test over the cloacal cavity and in the protuberant cone of the cloacal aperture. Both the latter species have their zooids arranged in a single circle around each common cloaca. In *A. crateriferum* the atrial lip is not close to the aperture as it is in the present species and *A. lunacratum* does not have the same bulging branchial sphincter and long siphon. In *A. lunacratum* the thoracic muscle bands, and in *A. crateriferum* the number of rows of stigmata are more numerous. The larvae of *A. clivosum* are in the same size range as those of *A. lunacratum* but larger than those of *A. crateriferum*. Larvae of the present species differ from *A. lunacratum* in having fewer epidermal vesicles and more ampullae.

Aplidium pantherinum (Sluiter, 1898) and its synonyms from South Africa (see Millar 1962) have a smaller larval trunk, and although they have narrow thoraces and about 17 rows of stigmata like the present species, the atrial tongue is not separate from the aperture.

Aplidium clivosum has possibly more variation in its external appearance than most other species of *Aplidium*. The size of the systems varies, as does the number per colony, the amount of embedded sand, the colour and the depth of surface depressions. These variations are not geographically based however and the whole range of morphological variations occurs in tropical as well as temperate waters.

In view of its wide range in Australian waters, it is probable that it will be found to occur in the Western Pacific. It is possible that some of the specimens assigned to *A. crateriferum* by Van Name (1918) from the Philippines are of this species.

Aplidium congregatum n.sp.
(Fig. 69)

DISTRIBUTION

TYPE LOCALITY: Queensland (North Stradbroke I., Point Lookout, coll. A. Rozefelds 17.11.78, holotype QM GH5584).

FURTHER RECORDS: None.

Specimens are found tucked into narrow rocky crevices at the type locality.

DESCRIPTION

EXTERNAL APPEARANCE: Sandy flat-topped lobes 1.5 to 2cm diameter around the upper surface, narrow toward the base where they are joined through common test. The edges of the flat upper surface fuse with adjacent lobes. A layer of sand adheres to the outside of the stalks and sides of the lobes, but is absent from the upper surface. Internally sand grains are scattered sparsely amongst the zooids. Zooids are crowded and parallel in the test. They may be in rows along each side of long canals that converge to the sessile cloacal apertures on the flat upper surface.

INTERNAL STRUCTURE: Zooids are long and narrow, up to 5mm long, of which the thorax and abdomen together comprise about half, and the thorax is about twice the length of the small abdomen. About 16 fine longitudinal muscles extend separately along the length of the zooid and are not gathered into bands on either side of the abdomen or the posterior abdomen. A distinct sphincter muscle is at the base of the 6 narrow, pointed lobes fringing the branchial aperture. The atrial aperture is at the anterior end of the dorsal surface with the forked atrial tongue extending from the anterior rim of the opening. Fine muscle fibres extend along the length of the atrial lip. The stigmata are in 11 rows of up to 12. The oesophagus is moderately long and narrow. The stomach is small and narrow with 12 longitudinal folds in its wall. There is the usual narrow mid-intestine, interrupted at the end of the descending limb of the gut loop by an oval posterior stomach. Small rectal caecaare at the proximal end of the rectum.

A large (4 or 5 oocytes) ovary is at the proximal end of the posterior abdomen and the testis follicles in a single or paired series are behind it in the long, narrow posterior abdomen. The holotype has up to 6 embryos being incubated in a developmental series lined up in the atrial cavity, tending to stretch the thorax longitudinally. Tailed larvae have a trunk 0.5mm long with the tail wound three quarters of the way around it. Conical median ampullae (4) alternate with the median adhesive organs. An arc of scattered epidermal vesicles (about 3 or 4 deep) is around the lateral line on each side of the adhesive organs and extending posterior to them along the dorsal and ventral border of the larval trunk. An ocellus and an otolith are present.

FIG. 68. *Aplidium clivosum* n.sp. — **a**, colony (QM GH5669); **b**, thorax and abdomen (QM GH5670); **c**, branchial aperture, atrial aperture and atrial lip showing sphincter muscles (SAM E2564); **d**, larva (QM GH5469). Scales: **a**, 1cm; **b**, 0.5mm; **c**, 1.0mm; **d**, 0.4mm.

REMARKS

The species is found in similar habitats and in the same geographic location as other flat-topped sandy, lobed species, all superficially resembling one another, viz. *Aplidium incubatum* n.sp., *A. directum* and *Botryllus stewartense* (see Kott 1990). The flat topped lobes of *A. congregatum* have more complex systems of crowded zooids than the others; *Aplidium directum* is distinguished by its tougher colonies with distinct circular systems, only 5 stomach folds and an atrial lip separate from the opening; *Aplidium incubatum* n.sp. tends to divide into separate lobes each with a single system, its zooids have 25 stomach folds, and the larvae have numerous vesicles but no ampullae.

The larvae of the present species resemble those of *A. opacum* which has investing, naked colonies; and *A. geminatum* n.sp. which has stalked heads with long cloacal canals converging to terminal cloacal apertures.

Zooids of the present species share some characters with those of *Aplidium fluorescum* n.sp., but both larvae and colonies are different.

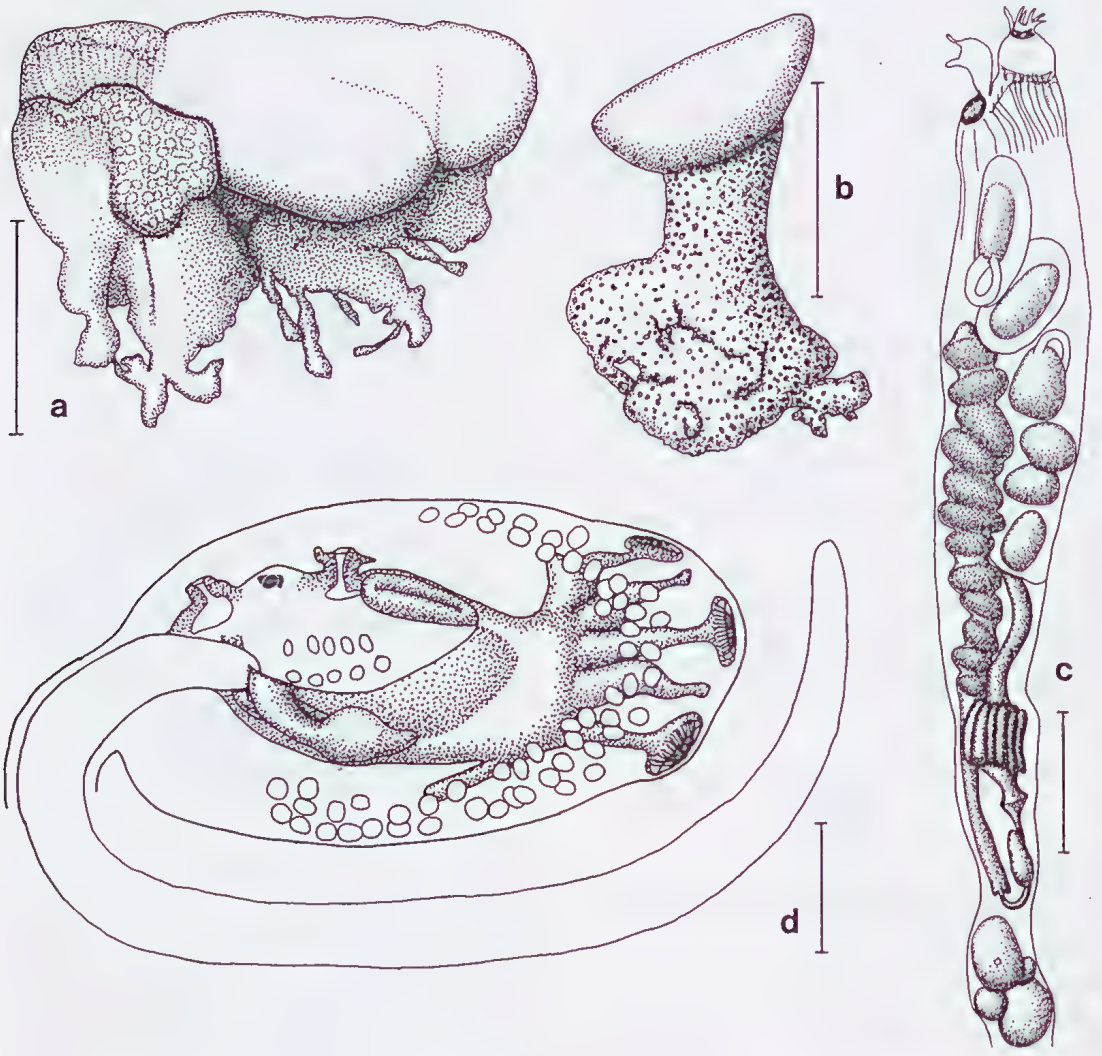


FIG. 69. *Aplidium congregatum* n.sp. (holotype QM GH5584) — **a**, **b**, colonies with positions of zooids shown in part of a colony lobe; **c**, thorax, abdomen, part of posterior abdomen and embryos in atrial cavity; **d**, larva. Scales: **a**, **b**, 1cm; **c**, 0.5mm; **d**, 0.1mm.

Aplidium coniferum Kott, 1963
(Fig. 70)

Aplidium coniferum Kott, 1963, p.102.

DISTRIBUTION

NEW RECORDS: South Australia (Elliston, SA E2580). Tasmania (off Devonport, AM E309; Huon Channel, TM D2074). Victoria (Bass Strait, QM G11861 GH5605, MV H462; Cape Everard, AM E6231–2; Gabo I., SAM E2592).

PREVIOUSLY RECORDED: New South Wales (Montague North, Twofold Bay, AM U3921 Kott 1963).

The species is known from depths to 400m (AM E6231–2).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are upright spherical to egg-shaped lobes, largely naked and without sand in the thin layer of smooth surface test. A basal hard sandy holdfast is probably rooted in sand. Sand is present in moderate concentrations internally. Zooids appear crowded in circular, oval to elongate systems, as well as some in double rows. However, the test is hard, whitish and almost opaque in preservative and it is difficult to determine the exact arrangement of the zooids. The shallow common cloacal cavities are relatively limited. They are surrounded by the fine, thread-like zooids, which are perpendicular at the surface, but cross one another posteriorly in the centre of the colony.

INTERNAL STRUCTURE: Zooids are narrow, and long. The branchial siphon is short, with 6 rounded lobes, but the prebranchial area is relatively long. The thorax and abdomen are each about 2mm even when contracted, and the posterior abdomen is many times that length. The atrial lip is small, pointed and arises from the body wall opposite the first row of stigmata. The atrial aperture is a small round opening, well removed from the lip, opposite the fifth or sixth row of stigmata. There is a pointed papilla posterior to the atrial aperture. About 2 longitudinal muscle bands are on the thorax and continue in wide bands along each side of abdomen and posterior abdomen. Stigmata are in 22 rows of 8 per row. The oesophagus also is long, and wrinkled when contracted. The stomach wall has 5 deep folds. There is a long duodenum and mid-intestine, and a small oval posterior stomach in the descending limb of the gut loop. Rectal caeca are not well developed.

A series of male follicles is in the posterior half of the posterior abdomen, and the small cluster of oocytes is just anterior to the male follicles. A large embryo sometimes is found being incubated in the atrial cavity (QM G11861). The larval trunk is 0.65mm long. It has lateral ampullae on each side near the base of the 4 median ampullae, the

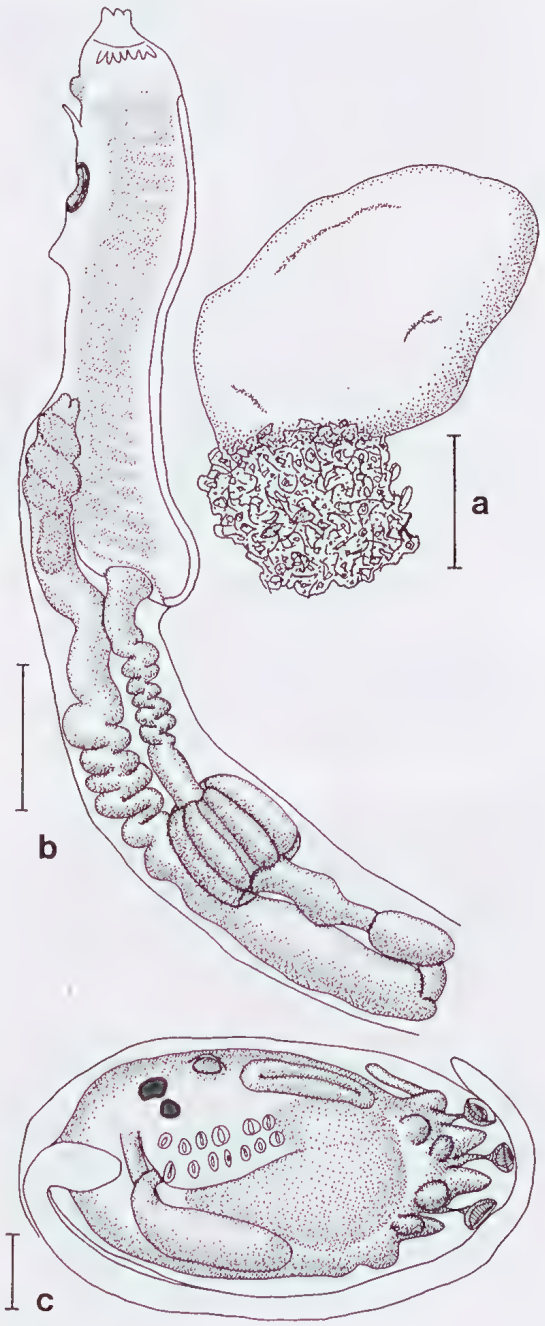


FIG. 70. *Aplidium coniferum* — **a**, colony (QM GH797); **b**, thorax and abdomen (MV H462); **c**, larva (QM G11861). Scales: **a**, 2cm; **b**, 0.5mm; **c**, 0.1mm.

latter alternating with the adhesive organs. The tail is wound about two-thirds of the distance around the trunk.

REMARKS

The large colony with embedded rather than surface sand and basal sandy holdfast, the long and narrow oesophagus, small and isolated atrial lip, and long thorax, are distinctive. The stomach folds are well formed, confirming that it is a species of *Aplidium* rather than *Synoicum*, which it resembles in having a dorsal papilla. The crowded systems distinguish the species from others such as *A. crateriferum* which, also has a long, narrow thorax, and separate atrial lip.

A colony from Bass Strait (AM E309) characteristic of this species, with sandy basal stalk, naked, upright, ovoid colony, and long narrow posterior abdomina criss-crossing internally, originally was assigned to *A. jacksoni* by Kott 1963. Despite her interpretation that the zooids were similar to those of *A. jacksoni*, this was not confirmed on reexamination of the specimen. The zooids are juvenile vegetative ones and neither stomach nor branchial sacs are developed.

Aplidium crateriferum (Sluiter, 1909)
(Fig. 71. Plate 13a–c)

Amaroucium crateriferum Sluiter, 1909, p.103.
Not Van Name 1918, p.163. **Not** Tokioka, 1967, p.40.
Aplidium crateriferum: Millar, 1975, p.242.

DISTRIBUTION

NEW RECORDS: Western Australia (Flinders Shoal near Onslow, QM GH5403; Exmouth, QM GH5398). Queensland (Capricorn Group, QM GH5158–9 GH5567; central section Great Barrier Reef, QM GH5422).

PREVIOUSLY RECORDED: Philippines (Sluiter 1909, Van Name 1918, Millar 1975).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are bulky, gelatinous and translucent but firm. The surface is smooth, and raised in high rounded ridges around irregular surface depressions. One to 3 large conical elevations with a terminal common cloacal aperture arise from each depression. Single apertures are sometimes more or less central but often at one or the other end. A shallow but extensive cloacal cavity is beneath the rela-

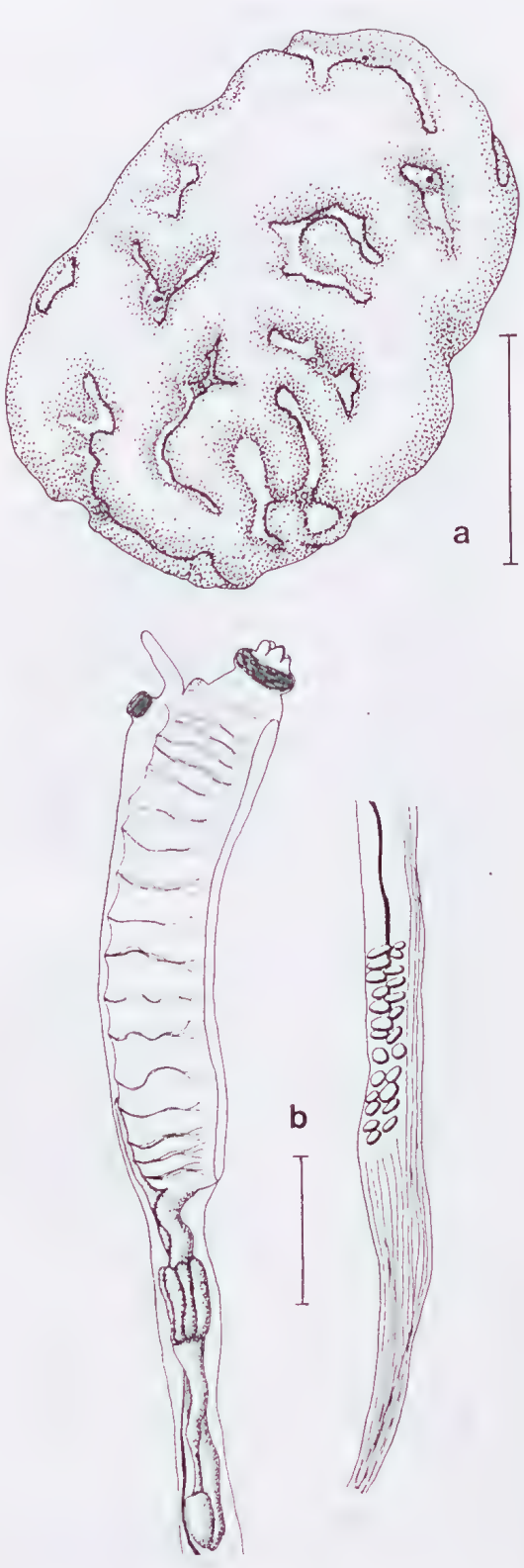


FIG. 71. *Aplidium crateriferum* — **a**, colony (QM GH5158); **b**, zooid (Heron I.). Scales: **a**, 2cm; **b**, 0.5mm.

tively thin surface test in the floor of each depression. Zooids surround each cloacal cavity, their branchial apertures at the base of the surface ridges, and protected by them. The atrial apertures are directed laterally to open into the cloacal cavity.

In some colonies a little sand is in the surface test around the apertures, but otherwise embedded sand is not present, and the surface is naked. In other colonies, sand is scattered throughout the test, amongst the zooids as well as in the zooid-free areas, and is on the external surface of the high ridges, although the surface of each depressed area is naked (QM GH5403).

Living colonies are said to be grey with red zooids, although photographs of specimens following their removal from the substrate are brown and yellow. In preservative the zooids, test and preservative are bluish-pink.

INTERNAL STRUCTURE: The zooids are long and thread-like, with the thorax (to 5mm) twice the length of the abdomen. The posterior abdomen is many times the length of the rest of the zooid. A long, conspicuous branchial siphon has a narrow bulging sphincter muscle at the top, near the base of the branchial lobes. This sphincter appears to have a blood sinus associated with it, and it is invariably pink and translucent.

There is a long pre-branchial area between the branchial tentacles and prepharyngeal groove and this effectively increases the length of the branchial siphon. The branchial tentacles cause a bulge about halfway down the siphon. Imperforate areas are anterior to the stigmata, and along each side of the endostyle. The atrial lip is usually a single pointed but quite fleshy lobe from the body wall anterior to the opening. The atrial aperture also has a sphincter muscle. About 15 fine longitudinal muscles are on the thorax and extend the whole length of the zooid. Fine transverse muscles are in the transverse vessels, but not in the parietal body wall. There are 18 to 21 short rows of up to 14 oval stigmata on the left and up to 10 on the right side of the branchial sac. The maximum number of stigmata (8 to 14) is in the fifth to eighth rows. Up to 4 more stigmata are on the left than the right. On the left the triangular dorsal languets are opposite the third to fourth stigmata i.e. almost halfway across the pharyngeal wall in the smaller, narrower zooids.

The short gut loop has the usual parts, with a slightly longer oesophagus than usual, and a relatively small stomach, with 5 distinct, deep folds in its wall. The posterior stomach also is short. Two conspicuous rectal caeca form a valve at the proximal end of the rectum. The posterior abdomen is long and thin. Two irregular longitudinal series of testis follicles are about halfway down it.

Single large embryos are in the thoraces of zooids collected in November, but not in May. The larvae are amongst the largest known for *Aplidium*, with the trunk 2mm long. The tail winds about three-quarters of the way around it. The long slender stalks of the 3 median adhesive organs are obscured by crowded epidermal vesicles which develop from the anterior part of the larval trunk.

REMARKS

The large, firm gelatinous colonies with surface depressions over the systems are one of the most conspicuous aspects of this species. The colonies are reminiscent of the colonies of *Lissoclinum patella* (see Kott 1980), *Synoicum castellatum* (see above) and *Aplidium clivosum*.

The sandy species *Aplidium caelestis*, with zooid openings protected by sand-filled swellings on the surface test, has similar narrow zooids with their atrial lip separate from the opening but they do not have the conspicuous surface depressions and circular systems of the present species.

The mostly temperate *Aplidium clivosum* also has similar zooids which open into deep surface depressions. However, it has zooids in double rows converging to the protruding common cloacal apertures, and fewer (14 to 18) rows of stigmata.

Sluiter's type specimen, from the Philippines, a large, fleshy mass, maximum dimension 10cm and up to 1.5cm thick with characteristic surface depressions and projecting cloacal apertures, closely resembles the present colonies. Millar (1975) describes similar colonies from this location. Other colonies from the type locality (Van Name 1918) are irregular with deep folds, but only shallow depressions, large systems with irregularly distributed zooids opening onto the flattened upper surface of the colony, and the surface thickly encrusted with foreign particles. These do not seem to be conspecific with the present species and are more like specimens of *Aplidium caelestis* (see below), which has similar zooids, but double row systems and embedded sand.

Tokioka's (1967) specimens from the Palau Is also appear to belong to some other species. They lack the characteristic surface depressions and the atrial lips extend from the upper rim of the opening rather than being separated from it as in the present species.

The narrow branchial sac, with wide bands of imperforate pharynx dorsally and ventrally is a characteristic of this species referred to by Sluiter (1909) in his description of the type. It should be noted that his figure of the branchial sac of the type (Sluiter 1909, pl.V7b) has been reversed — the larger number of stigmata and the dorsal languets are on the left, not on the right.

However, Sluiter appears to have overlooked the position of the atrial aperture and the sphincter muscles of both apertures, and miscounted the number of stomach folds (see Millar 1975). Sluiter has not always been accurate in his count of stomach folds (see *A. pantherinum*: Millar, 1962).

Aplidium depressum Sluiter, 1909
(Fig. 72)

Aplidium depressum Sluiter, 1909, p.102. Hartmeyer 1909, p.1499. Van Name, 1918, p.167. Kott, 1963, p.95. Kott and Goodbody, 1982, p. 515. **Not** Kott 1976, p. 60; 1981, p. 160.

DISTRIBUTION

NEW RECORDS: Queensland (Capricorn Group, QM GH890 GH916 GH2275 GH5680 GH5682 GH5690 GH5692 GH5693–702 GH5705–6).

PREVIOUSLY RECORDED: Queensland (Bargara — Kott 1963). Indonesia (Sluiter 1909; Van Name 1918). Hong Kong (QM G12796 Kott and Goodbody 1982).

These transparent, investing sheets, are probably more common than the records suggest. They are difficult to remove from the substrate and possibly are often overlooked by collectors.

DESCRIPTION

EXTERNAL APPEARANCE: Some colonies are thin, investing gelatinous sheets with a smooth upper surface, or they are irregular with the surface divided by shallow creases, or raised into convoluted ridges with common cloacal apertures along the ridges. One colony (QM GH5695) is a small cushion, trimmed to fit the back of a small crab on which it was found. In preservative, the small zooids are irregularly distributed and randomly oriented, usually lying at angles to one another. The test is translucent to glassy, firm and colourless. In life the zooids are maize yellow or orange to beige or pinkish beige, but they become white in preservative. *Prochloron* is found in the cloacal cavity and on the surface of some colonies (QM GH5682; see also Kott *et al.* 1984). Sand grains are sparsely scattered through the test, occasionally becoming crowded toward the base.

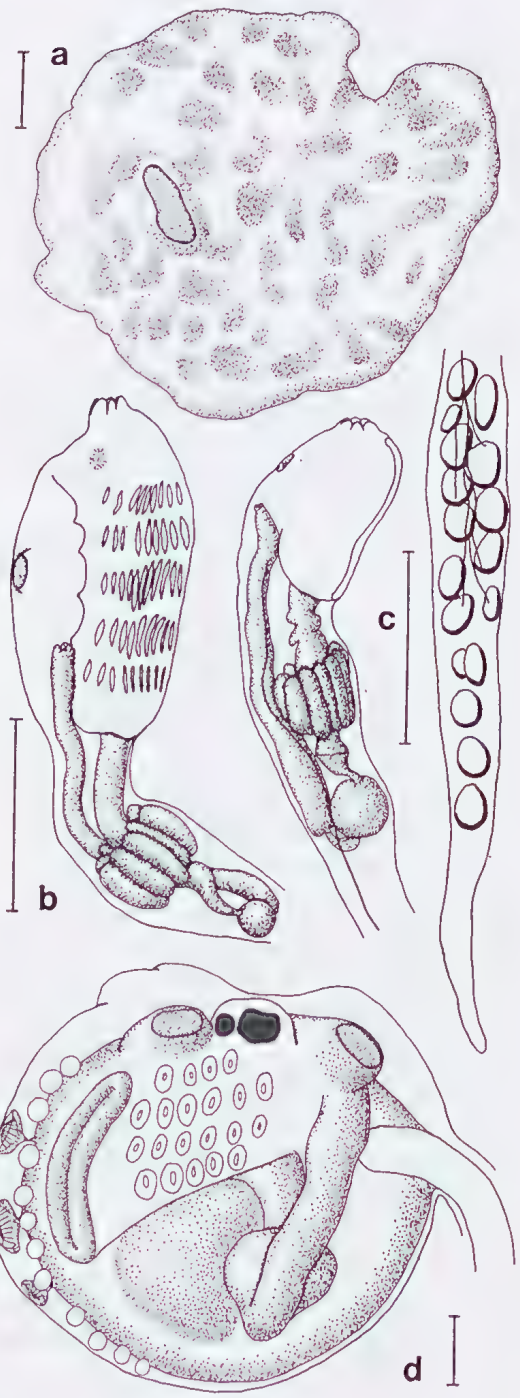


FIG. 72. *Aplidium depressum* — **a**, colony (QM GH890); **b**, **c**, thorax and abdomen, posterior abdomen separately (QM GH5697 QM GH5688); **d**, larval trunk (QM GH5693). Scales: **a**, 1mm; **b**, **c**, 0.5mm; **d**, 0.05mm.

Minute test cells appear as evenly spaced grains in the test.

INTERNAL STRUCTURE: Zooids are small, being no more than 3mm overall. The thorax and abdomen are of about equal length, and together are slightly shorter than the posterior abdomen which usually is relatively slender, tapering to its posterior end. The branchial aperture has 6 lobes. The atrial aperture is a single circular opening, sometimes on a short siphon, halfway down the thorax. There is no atrial lip. Stigmata are in 5 rows of up to 10, their length reducing at the dorsal end of each row.

The stomach wall has 11 distinct folds. A short thick duodenum and oval posterior stomach are in the post-pyloric part of the descending limb of the gut loop. The posterior abdomen is relatively short with a small ovary anterior to one or 2 rows of testis follicles. Up to 3 embryos are in the atrial cavity of colonies collected from Bargara in August and from the Capricorn Group from August to March (QM GH2276 GH5680 GH5683 GH5693–4 GH5702–3).

The larvae are amongst the smallest aplousobranch larvae known, with a spherical trunk only about 0.35mm in diameter. The greater part of the trunk is occupied by the developing adult organs — gut and pharynx. However, the cerebral vesicle is large in relation to the size of the trunk. A row of 7 or 8 epidermal vesicles is on each side of the median adhesive organs. Conspicuous test cells are in the surface of the larval test, tending to obscure the internal structure of the larva.

REMARKS

The principal characters of the present species are the transparent gelatinous test, the beige, yellow or pink zooids, the lack of an atrial lip, the 5 rows of stigmata, the relatively numerous stomach folds (12) and the minute spherical larval trunk.

The type specimen (Sluiter 1909) was gelatinous, with violet zooids seen through the test. Systems were not observed, although cloacal apertures were. The atrial siphon, without an atrial lip, is halfway down the thorax. Sluiter reported 9 rows of up to 14 stigmata in the branchial sac and numerous narrow folds in the stomach wall. Thus there is a discrepancy in the number of rows of stigmata and the colour between Sluiter's description and the newly examined material. There also is a discrepancy in the numbers of rows of stigmata in Van Name's (1918) specimens, with 6 or 7 rows of stigmata. Both Van Name and Sluiter may have had difficulty in determining the exact number of rows of stigmata in these small zooids, for most of the other characters conform with the newly recorded material. The ragged colony from Fiji (QM GH86) assigned to this species by Kott (1981), has been reexamined. It has, as reported, 8 rows of stigmata and a minute stomach with about 12 folds. There also is a narrow atrial lip from the upper border of the aperture which Kott overlooked. The colony is not conspecific with the present species. The colony (QM G12796) from Hong Kong (Kott and Goodbody 1982) appears to be correctly assigned.

Aplidium directum Kott, 1972
(Fig. 73)

Aplidium directum Kott, 1972c, p.246.

DISTRIBUTION

NEW RECORDS: Queensland (Dunwich, QM GH5517 GH5519; Cape Moreton, QM GH5614).

PREVIOUSLY RECORDED: New South Wales (Cronulla — AM Y1110–1 Kott 1972c).

The specimens are dredged from 6m to 140m from the sea floor.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are flat-topped, upright lobes, either separate or joined to a common base to form irregular, sandy masses up to 2.5cm high. The common base often is thin and keel-like and probably is buried in the substrate. Each separate lobe is about 1cm diameter, with a raised rim around its upper margin, surrounding a central depression containing a common cloacal aperture. Zooids are around the shallow common cloacal cavity beneath this depression.

Crowded sand particles are all over the surface of the colony and embedded throughout the test. Smaller sand grains only are on the surface in the terminal depression around the common cloacal aperture. In one extensive colony (QM GH5517) these smaller grains in the centre of each terminal lobe are black, apparently coal particles. Larger siliceous sand particles mixed with sparse black grains to give a grey colour are all over the remainder of the colony.

INTERNAL STRUCTURE: Zooids are thin and thread-like. The thorax and abdomen are of about equal length and together about 6mm. The branchial siphon has 6 distinct lobes. The atrial lip arises from the body wall just anterior to the aperture, which projects slightly on a short siphon

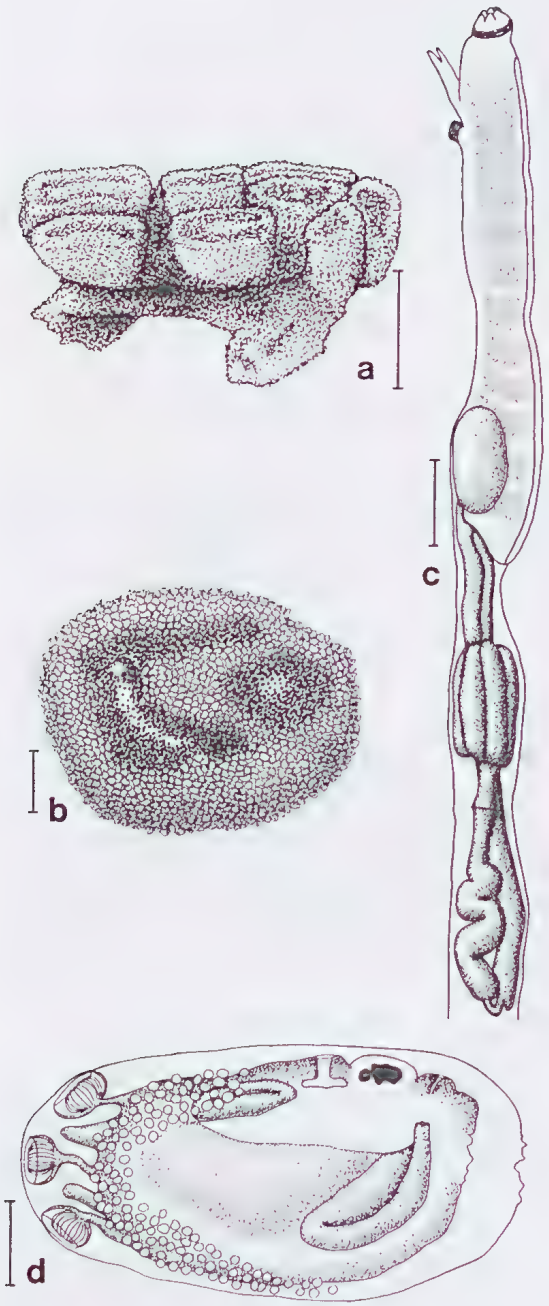


FIG. 73. *Aplidium directum* (QM GH5517) — **a**, colony; **b**, top of colony lobe showing depressions into which systems open with smaller grains of embedded sand; **c**, thorax, abdomen and embryo in atrial cavity; **d**, larval trunk. Scales: **a**, 1cm; **b**, 2mm; **c**, 0.5mm; **d**, 0.1mm.

with a sphincter muscle. The tip of the atrial lip is pointed or bidentate. There is a long unperforated band of pharyngeal wall both anterior and posterior to the perforated area. Short, wide stigmata are in 10 to 13 rows of up to 14 per row. The oesophagus is a narrow vertical tube. The stomach, also relatively long and narrow, has 5 well-defined folds. In extended zooids the post-pyloric part of the gut loop is relatively long. The descending limb has a long narrow duodenum and mid-intestine, but a relatively thick and slightly spiralling extent of gut in the lower one-third of the descending limb is in the position usually occupied by the short posterior stomach, well developed rectal caeca are at the proximal end of the rectum.

One or 2 embryos are in the posterior part of the atrial cavity in the material from Dunwich (collected in August), but not in the other specimen lot from Cape Moreton taken in the same month (QM GH5614). The larval trunk is about 0.5 to 0.6mm long. It has a conical median ampulla in each of the interspaces between the adhesive organs. An arc of epidermal vesicles is on each side of the median line around the anterior half of the larval trunk. The tail is wound about two-thirds of the way around the trunk. Ocellus and otolith are present.

REMARKS

The colony of this species resembles that of *Synoicum obscurum* and *Aplidium filiforme* n.sp. in the quantity of sand present, the size of the zooids, and the circular systems in lobes rising from the upper surface. *Aplidium filiforme* n.sp. is distinguished by having only 5 rows of stigmata a shorter branchial sac, a longer oesophagus, shallower stomach folds, 4 or 5 systems per colony lobe, and larvae without median ampullae.

The species is found in association with others superficially similar and sandy, viz. *Aplidium incubatum* n.sp., and *Botryllus stewartense* (see Kott 1985).

Larvae are not known from the New South Wales population — the type specimens of this species. However the similar morphology of these and the material from Moreton Bay indicate that they are conspecific.

Aplidium distaplium n.sp.
(Fig. 74)

DISTRIBUTION

TYPE LOCALITY: Victoria (Bass Strait, off Ninety Mile Beach, 10 km SW Seaspray, 560m off shore, calce-

narite reef 12m, fast currents, coll. J.E. Watson 21.3.80, holotype QM G12728; paratype QM G12729).
FURTHER RECORD: South Australia (Reevesby I., QM GH5602).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are solid, sandy irregular masses. Sand is crowded throughout, obscuring the small zooids and their arrangement. Zooids are tightly enclosed in the sandy test.

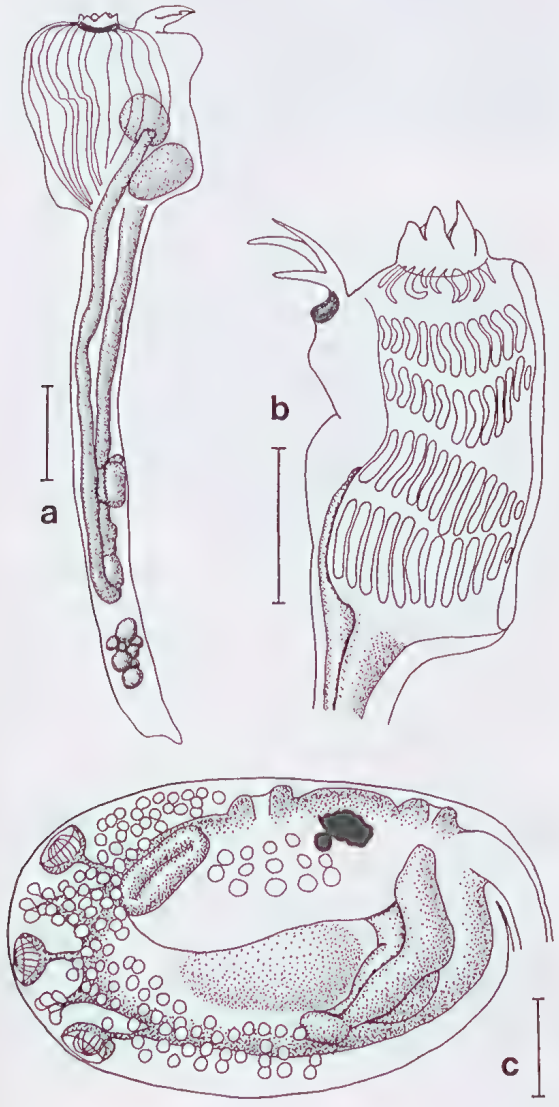


FIG. 74. *Aplidium distaplium* n.sp. — **a**, zooid, showing small posterior abdomen, long oesophagus (holotype QM G12728); **b**, thorax (paratype QM G12729); **c**, larval trunk (holotype QM G12728). Scales: **a**, **b**, 0.5mm; **c**, 0.1mm.

INTERNAL STRUCTURE: Zooids are minute, the thorax, abdomen and posterior abdomen together being about 4mm long, of which the abdomen is about half the length, the thorax and posterior abdomen being relatively short. The 6 branchial lobes are triangular and the siphon is short. A flat atrial tongue, undivided, bi-, or tripartite, extends out from the upper rim of the small aperture. About 15 muscle bands extend from the thorax, although they are fine, and the zooid is delicate.

Stigmata are in 4 rows of 12, and these rows are arranged in 2 pairs as in *Sycozoa* (see Kott 1990). The oesophagus is an unusually long vertical tube, and the 5-folded stomach is in the posterior half of the abdomen. The post-pyloric part of the descending limb of the gut loop (with the usual duodenum, mid-intestine and posterior stomach) is not as long as the oesophagus.

Sometimes the posterior abdomen is short, with only an ovary developed. In the male phase it is longer, with a double row of male follicles.

Embryos (up to 4) are incubated in the atrial cavity. The larval trunk is 0.52mm long. A large conical median ampullae with epidermal vesicles branching off it is in each interspace between the adhesive organs. Also there is a median dorsal ampulla and a ventral one. Epidermal vesicles are also scattered in an arc in the test around the anterior half of the trunk on each side. The tail is wound about three-quarters of the way around the trunk on each side of the median line.

REMARKS

The species resembles *A. solidum* in its solid hard sandy colony, although the larval trunk of the present species is longer. The presence of 4 rows of stigmata rather than 5, is unusual in this genus. In the related genus *Synoicum* only *S. bowerbanki* has a similar number of rows of stigmata (see above).

Aplidium elatum Kott, 1972

Aplidium elatum Kott, 1972b, p.177

DISTRIBUTION
NEW RECORDS: None.
PREVIOUSLY RECORDED: South Australia (Elliston Bay — SAM E905 E906 Kott 1972b).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies form tall, undulating fan-shaped lamellae, 1cm thick to 6cm high. Sand is present throughout, and the colony is hard. Common cloacal apertures are randomly

distributed over the surface and zooids are along each side of the cloacal canals converging to them. The surface test is raised slightly over the anterior ends of each of the zooids.

INTERNAL STRUCTURE: The anterior part of thoraces and the endostyles are orange in preservative. Zooids are about 3mm long, the thorax and posterior abdomen approximately equal in length and slightly longer than the abdomen. The branchial lobes are sharply pointed. The atrial aperture, opposite the fourth to sixth row of stigmata has a large lip divided into 3 large, muscular, leaf-like lobes from its anterior rim. The muscles in the atrial lip are longitudinal, extending down the centre of each lobe. About 12 longitudinal thoracic muscles extend posteriorly in 2 bands along each side of the zooid. Stigmata are in 8 rows of about 8. The stomach is short with about 15 longitudinal folds. The usual duodenum and mid-intestine interrupted by a posterior stomach comprise the post-pyloric part of the descending limb of the gut loop. Gonads are in 2 series in the posterior abdomen. Larvae are not known.

REMARKS

The sandy colonies of this species resemble those of *A. petrosum* n.sp. and *A. solidum*, although they are neither as branched, nor as extensive. The zooids, with their large atrial lips from the upper border of the opening, and 15 stomach folds resemble *A. opacum*, as does their arrangement in double rows of zooids converging to the common cloacal apertures.

Aplidium filiforme n.sp.
(Fig. 75)

Aplidium thomsoni: Kott, 1963, p.97 (part, specimens from Cockburn Sound). **Not** *A. thomsoni* Brewin 1950a.

DISTRIBUTION

TYPE LOCALITY: Queensland (Heron I. Blue Pools, coll. D. Parry 9.11.86, holotype QM GH5527; 9.11.85, paratype QM GH5528).

FURTHER RECORDS: Western Australia (Cockburn Sound — Kott 1963). Queensland (Capricorn Group, QM GH5511 GH5515 GH5523 GH5554–5).

DESCRIPTION

EXTERNAL APPEARANCE: The colony consists of upright, flat-topped sandy lobes that rise from the surface of a common basal mass, and aggregate together along their length through the sand attached to the surface test. They form a sandy platform up to 4cm in maximum dimension and about 1cm high. Groups of 4 or 5 systems open onto the upper surface of each lobe. In some colonies the tops of a number of lobes seem to fuse to form a cushion-like platform, with crowded systems opening on its upper surface. Each system consists of a wide, sessile cloacal aperture in the centre surrounded by branchial apertures obscured by the sand which is embedded in the test. Sand is not always present around the cloacal openings. The systems are usually quite conspicuous, even when sand is present on the upper surface, for the branchial apertures have small sand particles outlining them, while large sand grains are embedded around the outside of each system and in the centre around the common cloacal aperture. Living zooids have orange thoraces.

INTERNAL STRUCTURE: The zooids are minute, thread-like, about 0.3mm thick and about 7mm long. The thorax and abdomen together are about 3mm long and the posterior abdomen is at least twice that length. The branchial siphon is short although the branchial sphincter is large, bulging and conspicuous. The atrial aperture, with a short, stumpy tripartite lobe from the upper rim of the opening, is antero-dorsal. The 5 rows of stigmata have no more than 6 per row, although these could not be counted accurately. The oesophageal neck is longer than the post-pyloric part of the gut loop. The stomach has 5 distinct folds.

Ovary and testis are not mature in the one zooid at the same time. The ovary, when present, is a short distance from the posterior end of the gut loop — in the middle of the anterior third of the posterior abdomen. When the testis follicles are mature they are in a single row in the middle third of the posterior abdomen.

In the holotype colony 3 embryos are lined up in the atrial cavity. The most anterior of these is a tailed larva. The trunk length is surprisingly variable being 0.32 to 0.6mm. The adhesive organs are in the anterior mid-line. Epidermal vesicles, scattered 2 or 3 deep, in a long narrow arc along each side of the median line, branch off common stalks. Median vesicles also branch off one or 2 common stalks in each interspace between the adhesive organs. The arc of lateral vesicles extends well postero-ventrally and postero-dorsally.

REMARKS

This species, with its unusual lobed colony, small zooids with 5 rows of stigmata, 5 stomach folds, orange thorax and colourless abdomen and

posterior abdomen resembles *Aplidium mernooensis* (Brewin, 1956) from Chatham I., New Zealand and one colony from New Caledonia (Monniot 1987). Like the type, the specimens from New Caledonia have single systems of zooids in each lobe of the colony, and 8 branchial lobes. Although Brewin records the height off the substrate of *A. mernooensis* as only 2mm, its zooids are said to be 8mm long. Thus it appears that the base of the colony was embedded in the

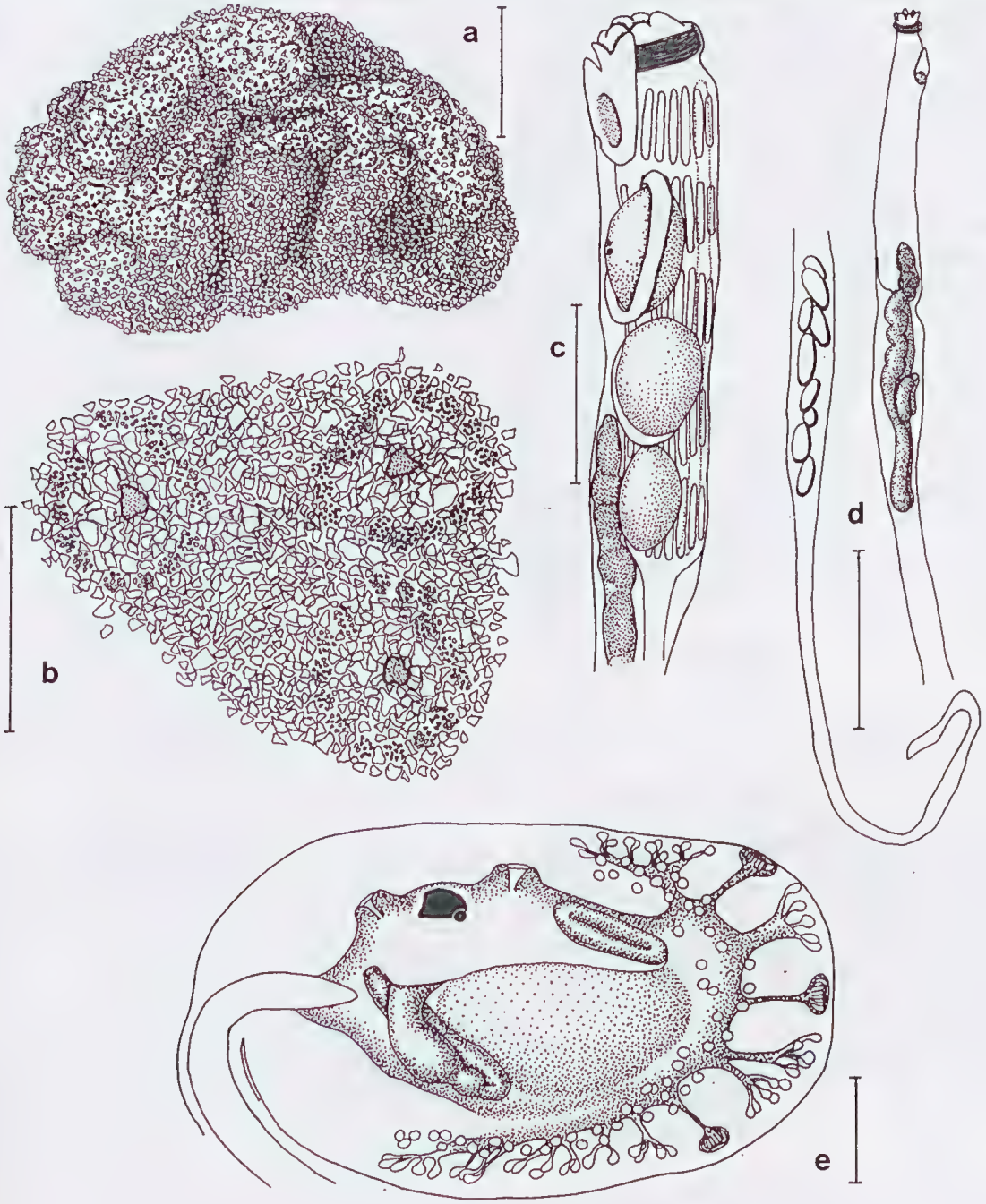


FIG. 75. *Aplidium filiforme* n.sp. — **a**, whole colony (QM GH5523); **b**, upper surface of colony lobes showing systems (QM GH5515); **c**, thorax with embryos in atrial cavity (QM GH5515); **d**, outline of whole zooid (QM GH5515); **e**, larval trunk (QM GH5555). Scales: **a**, 1cm; **b**, 5mm; **c**, 0.5mm; **d**, 1mm; **e**, 0.1mm.

substrate, and that it is much the same size as the present species. However, the present species has more than one system per colony lobe to distinguish it, and although *A. mernooensis* has sand externally, it lacks the embedded sand of *A. filiforme*. There also are more numerous stigmata in the Chatham I. colonies than in *A. filiforme*. Larvae from the New Caledonian colony (*A. mernooensis*: Monniot, 1987) have a trunk 0.65mm long with a wide lateral band of vesicles obscuring the anterior end of the trunk similar to the vesicles in *A. caelestis*, *A. clivosum*, *A. craterif-erum*, and *A. griseum* n.sp. The vesicles in the narrow lateral arc of the present species are less numerous and are spread over a smaller area at the anterior end of the trunk.

The large bulging branchial siphon known in *A. crateriferum* and *A. clivosum* is an unusual character not usually present in species with zooids as small as those in the present species. Monniot (1987) records a strong branchial spincter in the New Caledonian specimen. The larvae and zooids of the present species are among the smallest known in the genus.

Aplidium bacculum also has only 5 rows of stigmata, but its terminal heads, onto which zooids open, are naked, its systems less regular, its stalks longer and the oesophagus about two-thirds of the length of the abdomen.

Aplidium fluorescum n.sp.
(Fig. 76)

Aplidium multiplicatum: Kott, 1963, p.103 (part specimen from Sarina).

DISTRIBUTION

TYPE LOCALITY: Queensland (Heron I., NE Point, rubble fauna, low tide, coll. P. Kott 4.5.85, holotype QM GH5243; Heron I., NE reef, rubble fauna, coll. P. Kott 14.11.85, paratypes QM GH5244; coll. P. Kott May 1987, paratypes QM GH5245; NE Heron reef, coll. P. Kott 2.11.86, paratypes QM GH5246; Heron I., The Canyons, coll. P. Kott 13.11.85, paratypes QM GH5247).

FURTHER RECORDS: Queensland (Sarina, AM Y1448; Lizard I, QM GH5630; Capricorn Group, QM GH5318–24).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are small, rounded to dome-shaped cushions, to about 1cm in maximum thickness. Only the colony from Sarina (AM Y1448) forms extensive investing sheets. Living test is translucent, or opaque-whitish, with green fluorescent particles around the branchial apertures and in the surface test. These particles give an azure-blue sheen to the colony. Zooids are 'buff pink', or 'maize yellow' (Ridgeway 1886), or pinkish white, with an orange stomach. In preservative the zooids are beige to white and the test is almost opaque, or translucent to glassy. One of the living specimens (holotype) was described as a 'translucent fluorescent potato'.

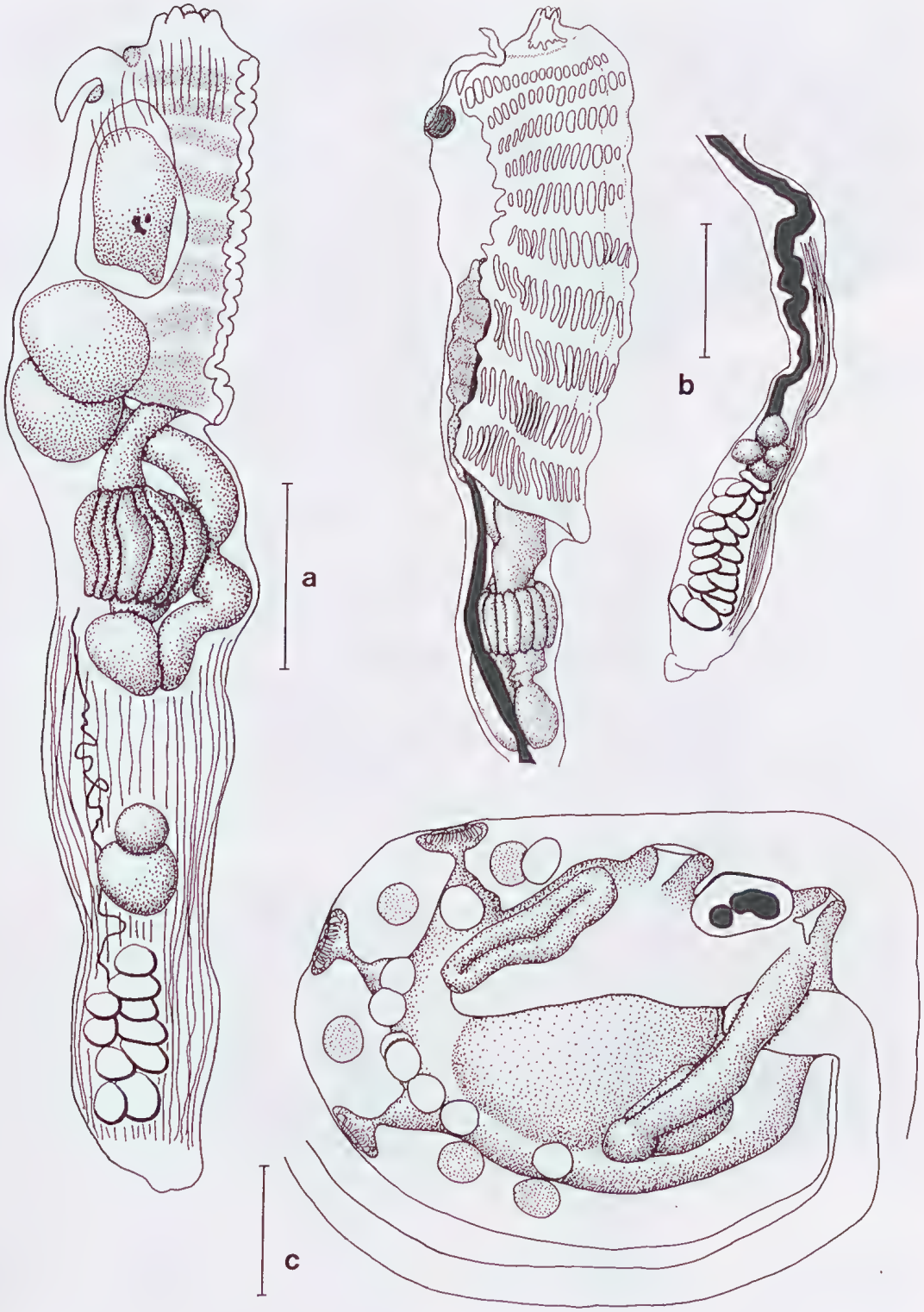
The test is firm and naked, and there is neither adherent nor embedded sand. The systems are circular, although often they are obscure in preserved specimens, with the zooids lying at various angles to one another in the firm test.

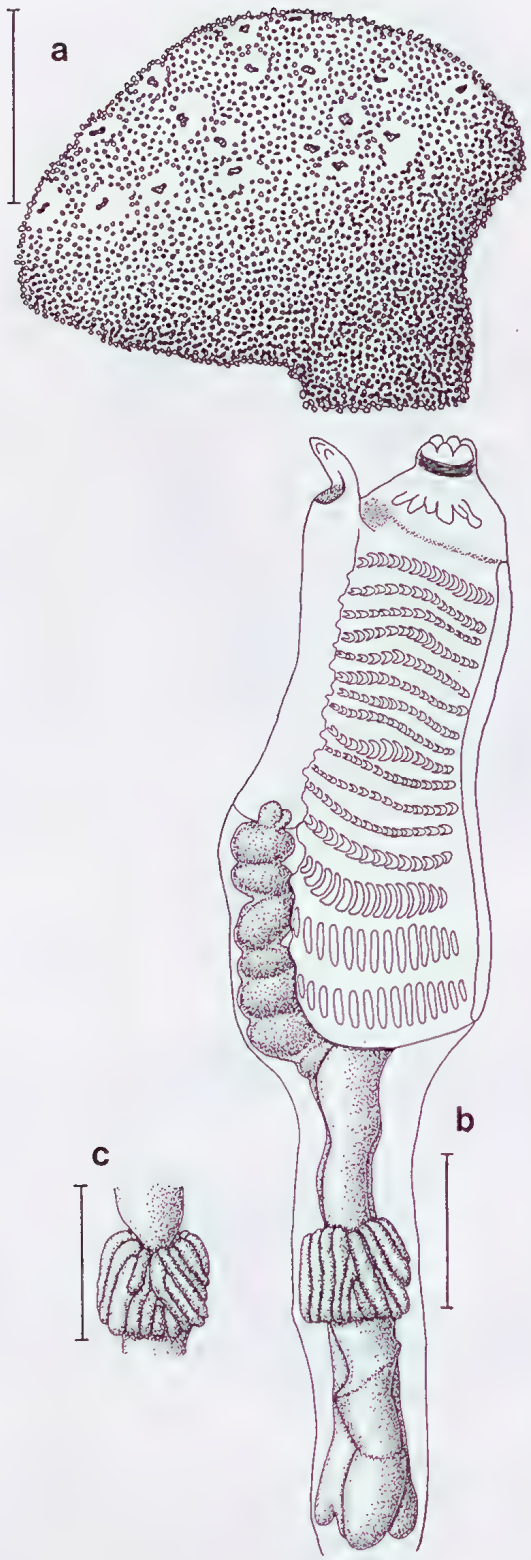
INTERNAL STRUCTURE: Zooids are about 6mm long when relaxed, the thorax and posterior abdomen of about equal length and the abdomen only a fifth of the total length. The branchial lobes are small and pointed and the branchial aperture almost sessile. The small and undivided atrial tongue arises from the upper border of the opening, which has a sphincter muscle. Fifteen to 20 longitudinal muscle bands are on each side of the thorax, and extend the length of the zooid, evenly spaced around it rather than forming a band on each side of the abdomen and posterior abdomen. The branchial sac has 10 rows of up to 16 stigmata. The moderately long stomach has 12 to 14 deep folds in its wall. The duodenum and proximal sections of the mid-intestine are wide, the latter being only slightly constricted from the oval posterior stomach.

Gonads are absent from the anterior half of the posterior abdomen, which is relatively short and thick and only occasionally larger than the thorax. The ovary is about halfway down the posterior abdomen, with the testis follicles in 2 irregular series posterior to it.

With only one exception (May 1987) the colonies from the Capricorn Group, all collected in April, May, August and November, have zooids with 2 or 3 embryos lined up in the atrial cavity. The larvae are small, the trunk being about 0.5mm long. They have the tail wound slightly more than halfway around the trunk. An ocellus and an otolith are present in the cerebral vesicle. There are 3 median adhesive organs on narrow stalks at the anterior end of the trunk, and up to 9 particu-

FIG. 76. *Aplidium fluorescum* n.sp. — **a**, **b**, zooids (paratypes QM GH5247 GH5244); **c**, larva (paratype QM GH5247). Scales: **a**, **b**, 0.5mm; **c**, 0.1mm.


a
b
c



larly large, spherical ectodermal vesicles separate from the lateral line on each side. Up to 3 embryos are in the Sarina specimens collected in August. Their larvae differ from the Capricorn Group ones only in having one more (total 10) epidermal vesicles in each of the lateral arcs. Ectodermal ampullae are never present.

REMARKS

The species is distinguished from others with naked colonies by its small zooids with the small atrial lip from the anterior rim of the opening and by the number of stomach folds and rows of stigmata. *Aplidium gelasinum* n.sp. is distinguished by its narrow thorax with only 8 stigmata per row. Its small larvae are also distinctive, and although similar ectodermal vesicles occur in other species (e.g. *A. multiplicatum*), there are fewer in the present species than in any others known.

Aplidium gastrolineatum n.sp.
(Fig. 77)

Aplidium flavolineatum: Kott, 1972b, p.177 (part, specimen from Waldegrave I.).

DISTRIBUTION

TYPE LOCALITY: South Australia (1km NW of Waldegrave I., Anxious Bay, 33°33'S, 134°46'E, rocky bottom, slow current, 23m, coll. S. Shepherd 11.5.71, holotype SAM E2584).

FURTHER RECORDS: South Australia (Pearson I. QM GH1292; Flinders I., QM GH2305).

DISTRIBUTION

EXTERNAL APPEARANCE: The holotype colony is an almost spherical cushion, 2.5cm diameter and 2cm high. It is fixed basally by a relatively broad sandy area. A thick layer of sand is present around the outer surface, being absent only from the circular depressed areas into which the systems open. Protruding common cloacal apertures are in the centre of each of these depressions. Zooids are in circles around each common cloacal aperture. The colony from Pearson I. lacks sand on the upper surface although it is present around the sides and base. It has the same circular systems and protuberant cloacal apertures. Sand is not embedded internally. The test is soft, white and translucent, and both colonies are distorted.

FIG. 77. *Aplidium gastrolineatum* n.sp. (holotype SAM E2584) — **a**, colony; **b**, thorax and abdomen; **c**, stomach from the left side. Scales: **a**, 1cm; **b**, 0.5mm; **c**, 0.5mm.

The zooids are tightly embedded in the test and a sheath of it, containing white opaque cells, clings to the zooids when they are removed. The living colonies are described as having a pink matrix with white zooids.

INTERNAL STRUCTURE: The zooids are robust, and the thorax and abdomen together are about 4mm long. The relaxed thorax is longer than the abdomen. The 10 fine longitudinal muscle bands on the thorax extend the length of the zooid in a wide band on each side. The 6 rounded branchial lobes are distinct. The atrial lip extends out from the upper rim of the aperture at the anterior end of the dorsal surface. It is thick and fleshy, with its tip divided into 3 rounded lobes. The stigmata are in 16 rows of up to 14. The stomach is relatively small, its diameter not markedly greater than that of the duodenum. Its wall has 24 mostly oblique folds. The stomach wall is more or less divided into 4 quarters with the folds in each quarter running obliquely to meet those of the adjacent quarters dorsally and ventrally, and in the middle of the mesial and lateral aspects. Three folds on the left side of the mid-dorsal line of the stomach, and 3 on the right of the mid-dorsal line do not reach the posterior end of the stomach, and further oblique folds in the middle of each side do not reach the anterior end. The duodenum and proximal end of the mid-intestine are wide. Rectal caeca are at the proximal end of the rectum.

Larvae are present in South Australian specimens collected in October (Kott 1972b, p.174 Fig. 30). They have a larval trunk 0.8mm long, and median and lateral ampullae between the adhesive organs. They lack epidermal vesicles.

REMARKS

The naked circular depressions each with a central protruding cloacal aperture, into which the systems open, are reminiscent of the surface of *Aplidium lunacratum* nom. nov. However, the latter species has only 5 stomach folds, and its atrial lip arises from the body wall anterior to the aperture, rather than from its anterior rim.

Aplidium incubatum n.sp. from Queensland also has circular systems opening into conspicuously naked surface areas. However, it has the surface of the colony partially divided, each division containing a system, and it has parallel longitudinal stomach folds.

Kott (1963, 1972a–c, 1975) erroneously assigned various specimens to the South African species *A. flavolineatum* Sluiter, 1898 on the basis of the number of gastric folds. Re-examination of these specimens has shown that they have other characters which distinguish them from one another, and from the African species (see *A. multilineatum* n.sp., *A. robustum* n.sp., *A. multiplicatum*, *A. uteute* and the present species). The present species is distinguished from the African *A. flavolineatum* by its oblique stomach folds and more numerous rows of stigmata. *Aplidium robustum* n.sp., which has similar numbers of stigmata and stomach folds, has more crowded systems and sessile cloacal apertures.

Aplidium gelasinum n.sp.
(Fig. 78)

DISTRIBUTION

TYPE LOCALITY: Queensland (far Northern Great Barrier Reef, Tydeman Reef, coll. AIMS Bioactivity Group 23.4.87 Q66 B2089, holotype QM GH5333).

FURTHER RECORDS: None.

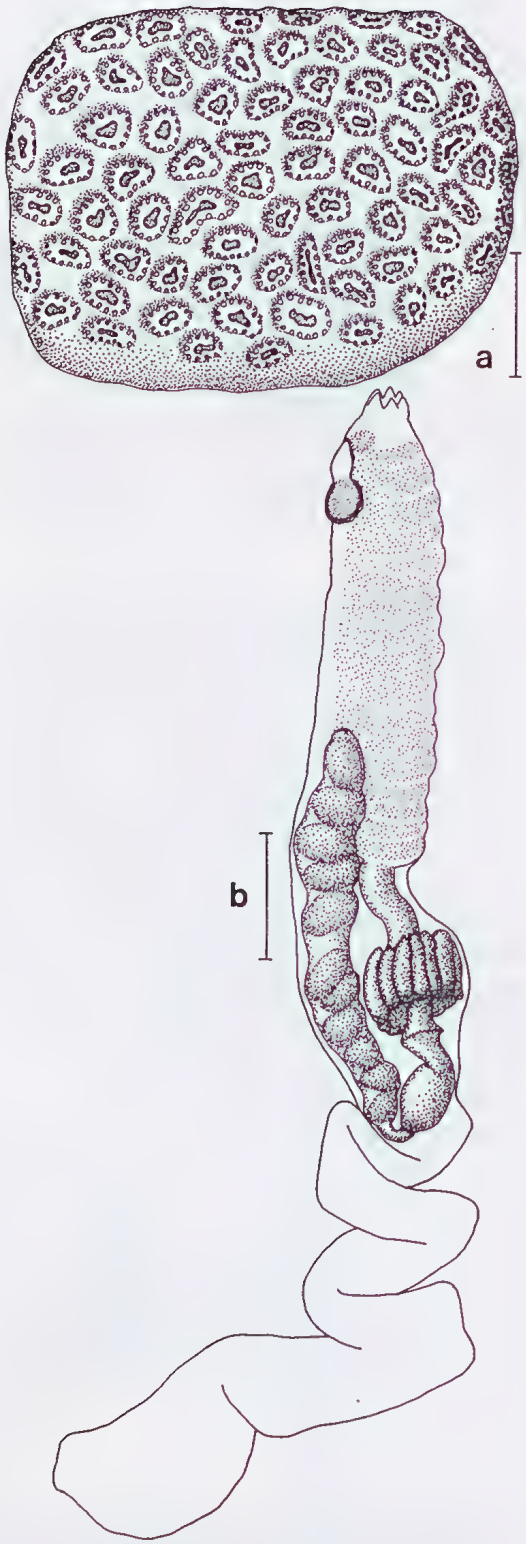
DESCRIPTION

EXTERNAL APPEARANCE: The colony is a flat-topped cushion; 7cm in maximum dimension and 1cm high. In preservative, it has a white opaque deposit in the surface test, which emphasises the circular zooid systems, being more opaque around the outside of each system where the surface is raised into a rounded rim and the test is thicker — not being interrupted by either zooids or cloacal cavity. Each system is about 3mm diameter. The cloacal cavity is circular with a central protuberant aperture. White deposit is concentrated in the surface layer of test. Internally the test is gelatinous and translucent. The zooids are firmly embedded and the sheath of test immediately surrounding each contains opaque, white cells. The specimen is reported to have been orange with orange zooids in life.

INTERNAL STRUCTURE: The zooids have a long posterior abdomen, although the thorax and abdomen together are only about 3mm. The atrial lip, from the upper rim of the opening, has from one to 3 points. Stigmata are in 16 rows of only about 8 per row. The small, relatively short stomach has 16 to 18 longitudinal parallel folds. Duodenum, mid-intestine and posterior stomach are of the usual form. When contracted the posterior abdomen is pulled up into a coil behind the abdomen. Gonads are not mature in this specimen, and larvae are not known.

REMARKS

Superficially, the regular circular systems in this opaque, white colony resemble *Distaplia prolifera* Kott, 1990 and *Morchellium pannosum*.



The crowded small, regular circular systems also resemble those of *A. lunacratum* nom. nov., although the latter species is distinguished by its external layer of sand between the systems and its fewer stomach folds. *Aplidium protectans* has circular systems, but 8 branchial lobes, more numerous rows of stigmata, and fewer stomach folds. *Aplidium fluorescum* and *A. uteute* have naked cushion-like colonies with circular systems, and numerous stomach folds like the present species. However they are softer colonies, have more stigmata per row and lack the surface depressions of the present species.

Aplidium geminatum n.sp.
(Fig. 79)

Aplidium australiensis Kott, 1963, p.111 (part, specimens from Port Lincoln and Western Port).

DISTRIBUTION

TYPE LOCALITY: South Australia (Price I., Avoid Bay, coll. S. Shepherd 9.4.87, holotype QM GH4175; Port Bonython jetty, 6m, coll. G.A. Powell, paratype QM GH4229).

FURTHER RECORDS: Tasmania (Bass Strait, SAM E2593); South Australia (Port Lincoln — Kott 1963); Victoria (Westernport — AM U3914 Kott 1963).

Although other records are from relatively shallow water, the specimen from Bass Strait is from 92m.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies consist of spherical to oval heads (3 to 6cm diameter), each on a thick, sandy stalk, occurring singly or in clumps. Long, more or less parallel, sometimes branching cloacal canals are along the sides of the heads. Zooids are arranged in double rows, a row along each side of the canal. The canals open to a number of large cloacal openings around the upper margin of the head, or to a few terminal apertures. A wide zooid-free strip of test is between adjacent double rows of zooids. A layer of sand is present on the outer surface of the colony, including the stalk. It is absent only from a bare area around the cloacal apertures on the top of the head. Sand is not present internally. The contracted, preserved colonies have a conspicuously transversely wrinkled sandy stalk.

FIG. 78. *Aplidium gelasinum* n.sp. (holotype QM GH5333) — a, colony from upper surface; b, zooid. Scales: a, 1cm; b, 0.5mm.

The anterior ends of the zooids are perpendicular to the surface, but the posterior ends curve down into the stalk and cross one another.

INTERNAL STRUCTURE: Zooids are robust, the thorax and abdomen together being about 3mm long when contracted. The posterior abdomen is longer and varies in length. About 12 longitudinal thoracic muscles extend posteriorly, forming a wide band along each side of the abdomen and posterior abdomen. The 6-lobed branchial siphon is short. The atrial aperture is a conspicuous, anteriorly oriented opening with a large, conspicuous atrial lip, deeply divided into 3 long pointed lobes, produced from the upper rim of the aperture. In some zooids 5 or 6 conical points project from the body wall in a transverse row just behind the atrial aperture. Longitudinal thoracic muscles lie between these projections.

Fifteen rows of 10 to 12 large, oval stigmata are present in the wide pharynx. The relatively long barrel-shaped stomach has 20 to 23 parallel longitudinal folds. The duodenal area is relatively long and roomy, and an oval posterior stomach is in the descending limb of the gut loop near its bend.

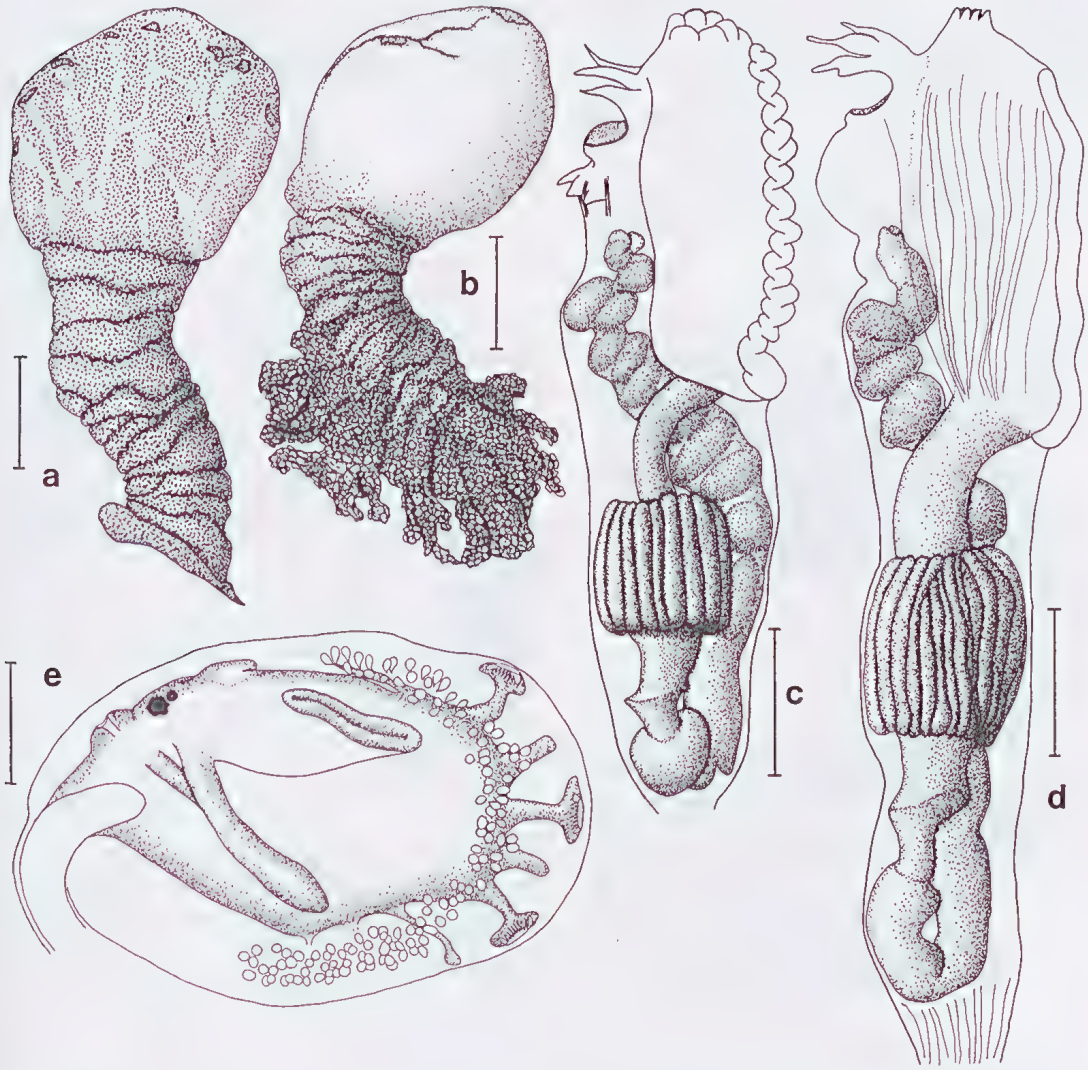


FIG. 79. *Aplidium geminatum* — **a**, **b**, colonies both showing thick sandy transversely wrinkled stalk (**a**, QM GH4175, indicating arrangement of zooids in vertical rows with a number of terminal cloacal apertures; **b**, SAM E2593 with 2 terminal cloacal apertures); **c**, **d**, thorax and abdomen (**c**, SAM E2593 showing transverse row of dorsal papillae; **d**, QM GH4175); **e**, larval trunk (AM specimen from Port Lincoln). Scales: **a**, **b**, 1cm; **c**, **d**, 0.5mm; **e**, 0.2mm.

Gonads are in the long posterior abdomen. Larvae are not present in the newly recorded specimens taken in February and April. However, they are present in the type material collected in September and November (see Kott 1963). The larval trunk is 0.9mm long with a band of numerous epidermal vesicles from the antero-lateral ridges along each side of the 3 median adhesive organs and the median ampullae that alternate with them.

REMARKS

The stalked colonies with parallel, double row systems down each side resemble *Sycozoa* and some *Distaplia* species (e.g. *D. australiensis*). Amongst *Aplidium* the species has some characters it shares with *A. australiense* and *A. brevilarvacium*, notably the stalked colonies with double row systems converging to relatively few common cloacal apertures. Of these two species, *A. brevilarvacium*, with its common cloacal aperture on the upper surface of the head, and relatively few cloacal canals, most closely resembles the present species. However, the zooids of both *A. australiense* and *A. brevilarvacium* are smaller than in the present species and they have fewer stomach folds, and fewer stigmata. There are other differences in the size and shape of the colonies (see species descriptions below). A conspicuous character of the present species is the large atrial lip with its 3 long pointed lobes.

The protruding dorsal papillae in a transverse row behind the atrial aperture are at the level of, and may be homologous with, the dorsal median papillae present in species of *Polyclinum* and *Synoicum*.

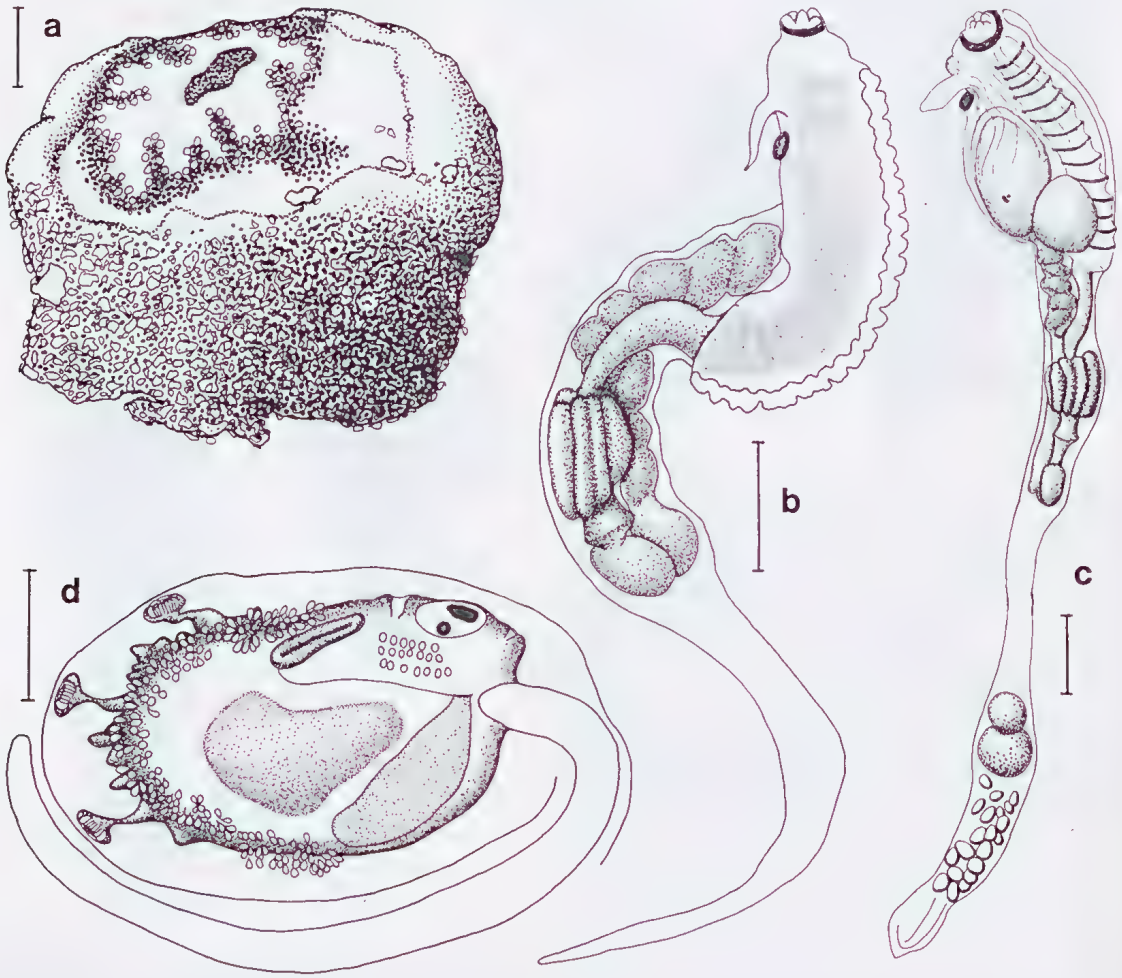


FIG. 80. *Aplidium griseum* n.sp. — **a**, colony (QM GH5171); **b**, **c**, zooids (holotype QM GH5212 GH5172); **d**, larva (QM GH5213). Scales: **a**, 2mm; **b**, **c**, 0.5mm; **d**, 0.2mm.

The larvae resemble those of *Aplidium opacum* with a band of numerous epidermal vesicles along each side of the median adhesive organs, similar numbers of stomach folds, and a similar large atrial lip. The form of the colonies and systems differ from those of the present species, and the zooids have fewer rows of stigmata.

Aplidium griseum n.sp.
(Fig. 80)

DISTRIBUTION

TYPE LOCALITY: Queensland (Heron I., under rubble, near reef edge, low tide, coll. P. Kott May 1985, holotype QM GH5212; May 1985, 1987, paratypes QM GH5214 GH5215).

FURTHER RECORDS: Queensland (Capricorn Group, QM GH5171–3 GH5213 GH5216–7 GH5529–31 GH5613 GH5668).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are small, upright (to 1.0cm high), almost cylindrical (to 1cm diameter), flat-topped lobes. Embedded sand is crowded in the lower half of the lobe and becomes less crowded in the top half. Sand is present also on a ridge around the periphery of the upper surface of each lobe, and is crowded into a line around each system where the branchial apertures open at the base of marginal ridges. As well as the peripheral ridge around the upper surface of each lobe the marginal ridges are on the upper surface separating the systems from one another. The thin threadlike zooids are in irregular or circular systems around 2 or 3 sessile common cloacal apertures on the upper surface of each lobe. Radial extensions from the peripheral test extend in toward the centre of a system and have zooids along each side. The regular circles of zooids are thus interrupted and the number of zooids in a system is increased.

Living colonies are 'Indian-', or 'prune purple' to 'blackish' or 'light translucent lavender', or 'Prouts brown' externally and 'poppy red' internally. Zooids are 'vermilion' (see Ridgeway 1886). In life, red pigment in the atrial lips can be seen through the translucent test. The preservative sometimes is stained reddish-orange. Brown spherical cells are in the test of preserved specimens.

INTERNAL STRUCTURE: The delicate zooids have fine longitudinal muscles extending their whole length. The branchial lobes are rounded and petal-shaped. The atrial lip from the body wall anterior to the small rounded aperture is narrow and pointed. Opaque brown pigment particles are around the zooid openings and along the endostyle. These particles probably cause the red colour in the living zooids. The thorax, is longer than the abdomen with 13 rows of up to 16 stigmata per row. The small stomach in the middle of the abdomen has 8 or 9 deep folds in its wall. Of these 2 or 3 do not extend the whole length of the stomach. Caeca at the proximal end of the rectum form a rectal valve.

The posterior abdomen is long and thin, with an anterior ovary and double row of male follicles in its posterior two-thirds.

In specimens collected in May, a tailed larva and a second less advanced embryo are in the atrial cavity. The larval trunk is 0.85mm long, with small, pointed median ampullae in each interspace between the 3 adhesive organs. The whole anterior end of the trunk is obscured by an arc of scattered epidermal vesicles in the larval test along each side of the mid-line.

REMARKS

The species is distinguished by its upright colonies, small stomach with 8 folds in the stomach wall, relatively wide thoraces with numerous (16) stigmata per row, and delicate musculature in the body wall.

Incomplete stomach folds that do not extend the full length of the stomach are known in other species of this genus e.g. *Aplidium multipapillatum* Millar, 1975. The latter species also has a similar number of stigmata in each row, but it has more stomach folds than the present species. Colonies resemble those of *Aplidium craterif-erum* and *A. clivosum*, with systems opening into depressions on the surface of the robust colonies. However, the present species has more stomach folds.

The larva is like that of *Aplidium ritteri* with scattered vesicles around the anterior end, although the trunk of the present species is larger.

Aplidium incubatum n.sp.
(Fig. 81)

DISTRIBUTION

TYPE LOCALITY: Queensland (Point Lookout, in crevices on rocky platform, high tide, coll. P. Kott 12.5.87, holotype QM GH5309; paratypes QM GH5310).

FURTHER RECORDS: Queensland (Point Lookout, QM GH5311–2; Cape Moreton, QM GH5615).

The records are from 0 to 10m, from rocky substrates.

DESCRIPTION

EXTERNAL APPEARANCE: The colonies vary in shape from extensive plates up to 2cm in maximum diameter to upright mushroom-shaped more or less flat-topped lobes (up to 1cm high). Sometimes the base of the colony is drawn out into a long, flattened extension which fits into narrow crevices and sometimes narrow stolons join the separate lobes of a colony to one another, or function as root-like processes fixing the colony in the substrate. Small circular systems of up to 10 zooids, and 5mm diameter are crowded in the colony and open on the upper surface. Large, sessile common cloacal apertures are in the centre of each system. The test above the systems is naked, pinkish-white and translucent. Sometimes sand is on the surface test separating single, or groups of, systems from one another.

Sand also is present on the surface test around the sides and base of the colony and varying amounts are embedded in the test amongst the zooids. The test is firm and transparent in preservative. In life, colonies are pink around the periphery of the systems, or red-orange with orange or salmon coloured zooids.

INTERNAL STRUCTURE: The zooids are robust, but the thorax and abdomen together are only about 2mm long, the thorax slightly longer than the abdomen. The posterior abdomen occupies about half the length of the zooid. The 6 branchial lobes are large and fleshy, with a small, pointed papilla in the centre of each lobe, sometimes

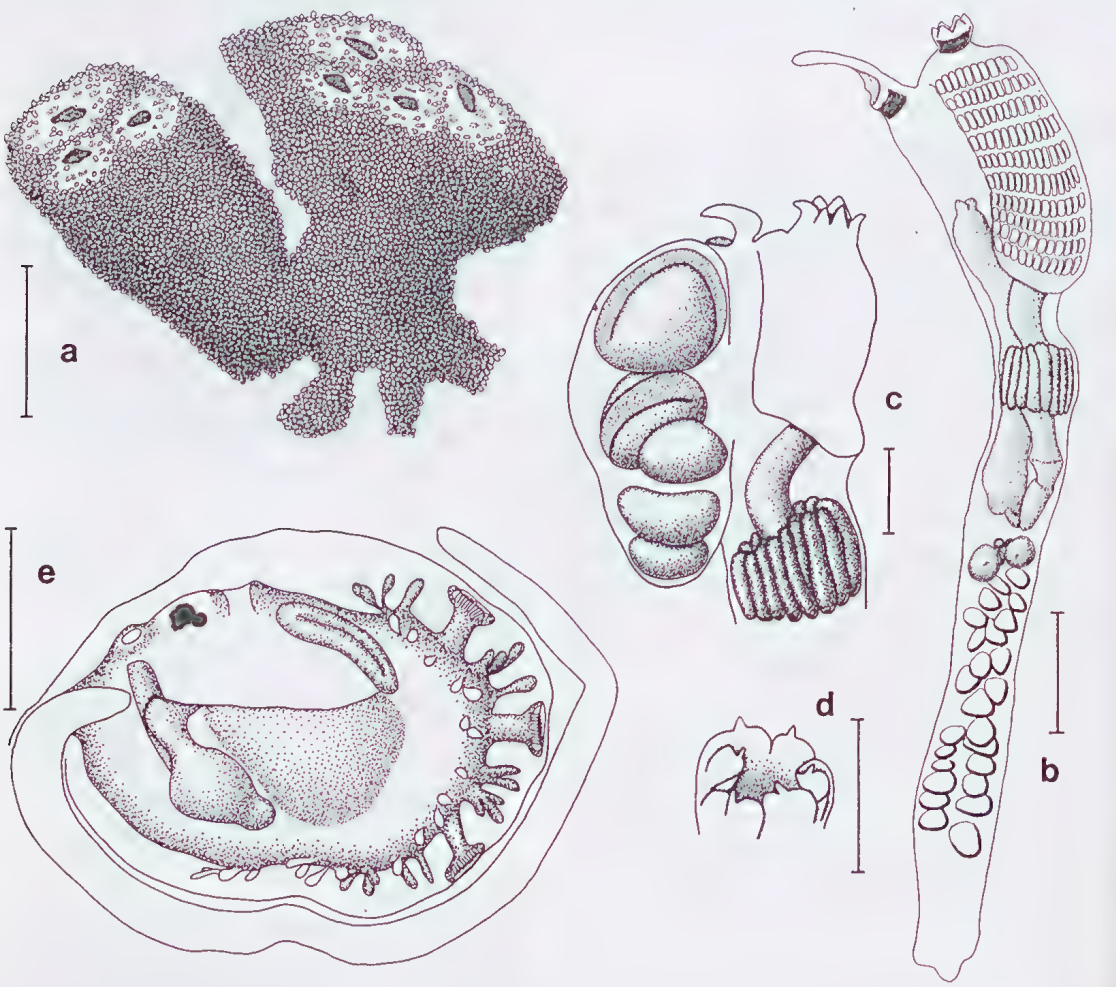


FIG. 81. *Aplidium incubatum* n.sp. — **a**, colony (holotype QM GH5309); **b**, whole zooid (paratype QM GH5310); **c**, anterior part of zooid with embryos in brood pouch (holotype QM GH5309); **d**, branchial lobes (paratype QM GH5310); **e**, larva (holotype QM GH5310). Scales: **a**, 5mm; **b–d**, 0.5mm; **e**, 0.2mm.

slightly depressed into its surface. The atrial lip is produced from the upper rim of the opening and is single or divided into 2 or 3 lobes. Twelve thick, conspicuous muscles are in the thoracic wall and extend the length of the zooid in a narrow band on each side. Broad, rectangular stigmata are in 9 or 10 rows with up to 15 per row.

The stomach has 25 folds in its wall. The oesophagus and post-pyloric part of the descending limb of the gut loop are of moderate length, an ovary is in the anterior part of the abdomen behind the gut loop, and the male follicles are in a long, irregular and rather loose bunch occupying most of the posterior abdomen.

Zooids of the holotype each have a large brood pouch, constricted off from the postero-dorsal corner of the thorax, with up to 6 embryos in a developmental sequence, lined up in it. The most advanced tailed larva is uppermost. It has a trunk 0.55mm long, and a tail wound three quarters of the way around it. About 16 epidermal vesicles are in a single arc on each side of the mid-line around the anterior half of the trunk.

A total of 7 epidermal vesicles in the interspace between the upper and middle adhesive organs branch off 2 common basal stalks, and 5 branch of 2 basal stalks in the lower interspace.

REMARKS

A. uteute and the present species have circular systems, a brood pouch and similarly arranged epidermal vesicles. However, the larvae of the present species lack the median vesicles, the zooids have fewer stomach folds and fewer stigmata per row than *A. uteute*, and the test has embedded sand, which *A. uteute* does not have. *Aplidium ornatum* n.sp. has sand around the border of the colony, like the present species, but is distinguished by its more numerous and scattered larval epidermal vesicles and lack of a brood pouch.

Aplidium inflorescens n.sp.
(Fig. 82)

? *Aplidium opacum* Kott, 1963, p.108 (part, lobed specimen from Balnarring Beach).

DISTRIBUTION

TYPE LOCALITY: South Australia (SW Point, Grindal I., NNE Cape Catastrophe 18m, coll. L. Hobbs, H. Brandon on RV *Ngeria* 29.9.89, holotype SAM E2588).

FURTHER RECORD: Victoria (? Balnarring Beach — AM Y1401 Kott 1963).

DESCRIPTION

EXTERNAL APPEARANCE: The colony consists of multiple stalked heads branching from a sandy common base. Heads are hemispherical to 2.5cm diameter, and the thick stalks are of slightly less diameter and up to 1.5cm long. Sparse sand is embedded in, and is present on the surface of, the stalk, increasing in abundance toward the base. Sand is absent from the head. Zooids are arranged in double rows converging to a few common cloacal apertures on the terminal surface of each lobe.

INTERNAL STRUCTURE: The zooids are of moderate length, the thorax and abdomen together being about 4mm. The posterior abdomen is long and thread-like. The atrial lip is from the anterior rim of the aperture. It is undivided and usually its median longitudinal muscles are contracted causing the edge to be frilled. Stigmata are in 15 rows with 14 or 15 per row. The oesophagus has a slight prestomach enlargement. The stomach wall has 20 folds.

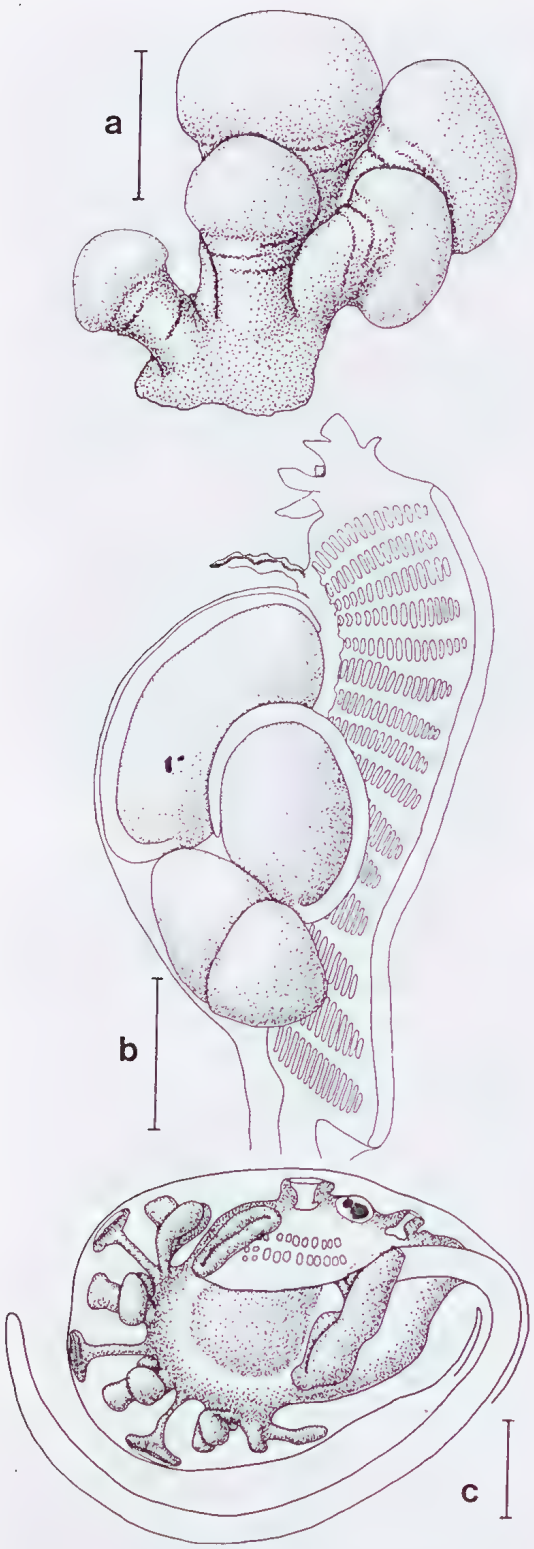
Up to 4 embryos are crowded in the atrial cavity of the type specimen. In the contracted zooid this causes the dorsal surface to protrude. Larvae are large, the trunk almost 0.9mm long, with median and lateral ampullae alternating with the adhesive organs. There are no epidermal vesicles.

REMARKS

The colony of this species with its thick basal stalks and longitudinal rows of zooids converging to terminal cloacal apertures, resembles *Aplidium geminatum*, which also has a similar number of stomach folds, and is recorded from South Australian waters. The present species lacks the layer of external sand characteristic of *A. geminatum*, and its stalks are shorter, thicker, more branched and not so wrinkled. Further, the larvae of the present species lack the arc of crowded epidermal vesicles found in *A. geminatum*. They have, instead, well-formed lateral ampullae.

Aplidium brevilarvacium has similar cloacal systems but the heads are smaller and sandy, the stalks thinner and longer, and the stomach has only 10 folds, thus is readily distinguished from the present species.

The larvae of the present species are similar to those of *A. coniferum*, which is distinguished by its large undivided upright colony, and its zooids with only 5 stomach folds. *Aplidium lodix* n.sp. has a similar larva without vesicles, and with median and lateral ampullae, but its colonies are extensive and investing with branching rows of



zooids converging to the randomly distributed common cloacal systems.

The colony assigned to *A. opacum* by Kott (1963) is in vegetative condition, and although the colony resembles that of the present species, zooids are not available to confirm its identity.

Aplidium jacksoni Kott, 1963
(Fig. 83)

Aplidium jacksoni Kott, 1963, p.110 (part, holotype).

DISTRIBUTION
NEW RECORDS: None.
PREVIOUSLY RECORDED: New South Wales (Port Jackson — AM U3917 Kott 1963).

DESCRIPTION
EXTERNAL APPEARANCE: The colony is a circular slab, about 12cm diameter and 2cm thick. Sand is embedded thickly in the surface layer of test, but is not present externally adhering to the outer surface. Sand is sparse in the lower half of the colony. Circular cloacal spaces are just below the surface, covered over by a thin layer of test, and with large, irregular, sessile cloacal apertures in the centre. Zooids are in wide circles of about 8 to 12 surrounding the cloacal cavities. Each branchial aperture opens on or inside a small upstanding papilla, which has one or more of the ventral branchial lobes embedded in it.

INTERNAL STRUCTURE: The zooids are robust, with a short thorax and a long posterior abdomen. The atrial aperture has a small pointed lip from the upper border of the opening. Branchial lobes are small and pointed. Stigmata are in 12 rows of 16. The wide stomach is relatively short with about 12 regular, parallel longitudinal folds. Two rows of male follicles are in the long, robust posterior abdomen. Larvae are not known.

REMARKS
Although it is not impossible that *A. jacksoni* occurs in Bass Strait, a naked, stalked, colony from off Devonport (Tasmania), assigned to this species by Kott (1963), is not conspecific. It is in the vegetative phase, and appears to be a colony of *A. coniferum* (see above).

FIG. 82. *Aplidium inflorescens* n.sp. (holotype SAM E2588) — **a**, colony; **b**, thorax showing embryos being incubated; **c**, larva. Scales: **a**, 2cm; **b**, 0.5mm; **c**, 0.2mm.

The present species is characterised by its distinct circular systems, with the position of the branchial openings indicated by a papilla on the surface of the colony. The zooids have some characters in common with *A. triggsense* which, however, has more crowded zooids and sand embedded in the basal layer of test rather than the surface.

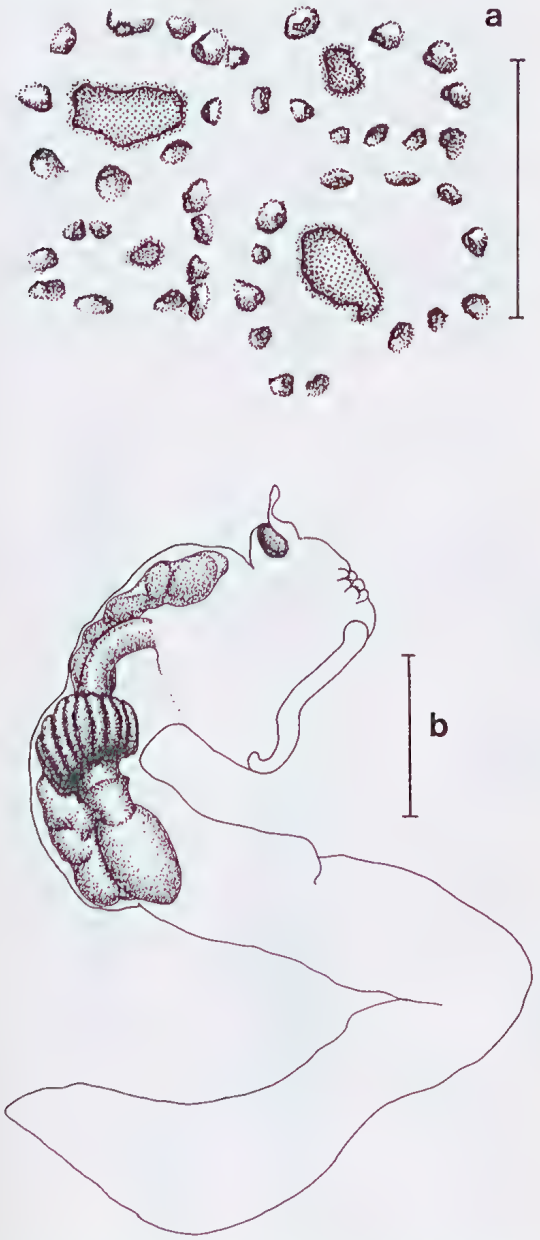


FIG. 83. *Aplidium jacksoni* (holotype AM U3917) — a, surface of part of colony showing large sessile common cloacal apertures surrounded by the branchial apertures on small papillae; b, zooid. Scales: a, 5mm; b, 0.5mm.

Aplidium lenticulum n.sp.
(Fig. 84. Plate 13d–f)

DISTRIBUTION

TYPE LOCALITY: Queensland (Heron I. under coral slab 3m, coll. N. Coleman 26.11.74 AMPI 141, holotype QM GH5060. Heron I., coll. P. Fredrickson May 1975, paratype QM GH5061.

FURTHER RECORDS: Western Australia (Carnac I., QM G9475; Rockingham, QM GH5457). South Australia (Topgallant I, QM GH941). Queensland (Capricorn Group QM GH1497).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are robust sheets or slabs up to 20cm in maximum extent and to 2cm thick. The upper surface is divided into flat-topped, circular, oval or polygonal zooid-free elevations of varying diameter up to 1cm. These are separated from one another by narrow depressions. In the base of each depression is the thin layer of test forming the roof of the common cloacal canals. The zooids open along each side of these common cloacal canals in the angle between the base and sides of the depression. The ventral surface of each zooid is in the solid test beneath each elevated area, atrial apertures are in the base or sides of the cloacal canals and atrial lips are in the test above the canals. Sand is packed in the lower half of the colony and around the outer margin, but the upper half of the colony is completely or partially free of sand.

The sand occasionally spreads from the lower half of the colony into the test around the zooids and above them, into the outer margin of each elevation, thus protecting the branchial openings. Sometimes some small clumps of sand are scattered in the surface of each elevation and these may also be present in small papillae projecting from the upper surface. The sand is also occasionally present in the surface test above the cloacal canals, and around the large common cloacal apertures which appear to occur randomly at the junctions of cloacal canals. The cloacal apertures are conspicuous, projecting from the surface of the colony, with a large cloacal chamber beneath them. Brownish oval bodies (about 0.1mm long) are in the test especially crowded around the cloacal canals, in their base, walls and roof. They become more sparse toward the base of the colony. These contain granular material, but they do not appear to be faecal pellets.

In life colonies are said to have been black, greenish-black, red, aqua-blue (South Australian

specimens) translucent gels, although all photographed specimens appear to be cream and red.

INTERNAL STRUCTURE: Zooids are robust. The thorax and abdomen are together about 3mm long, and of about equal length, but the posterior abdomen is at least twice the length of the rest of the zooid.

The branchial siphon is long with a large sphincter around the base of the lobes. Fine longitudinal muscle bands number about 12 on the thorax. The atrial lip arises from the body wall opposite the first row of stigmata, and the atrial siphon surrounded by a sphincter muscle, is opposite the fifth or sixth row. The tip of the atrial lip is invariably entire and pointed. The atrial lip is particularly long and broad. Zooids located in the vicinity of a cloacal aperture have their atrial lips inserted into the test around the rim of the opening.

An extent of unperforated pharynx is between the tentacular ring and the first row of stigmata. Also, bands of unperforated pharynx lie along each side of the endostyle, the perforated part being a relatively narrow part of the dorsum of the pharynx. Stigmata are in 16 to 20 rows of up to 8 per row.

The stomach has 5 folds although when inflated only slight anterior and posterior protrusions remain.

The posterior abdomen is long and thin, the test follicles in one or 2 series are usually separated from the posterior end of the abdomen by an interval of various lengths. The ovary is at the anterior end of the male follicles. It increases in size as it moves up into the atrial cavity from 0.7 to 1mm. It is a long, pointed, egg-shape, rounded at one end and tapering to a blunt point at the other. Embryos are present in the atrial cavities of specimens from Rockingham (collected in

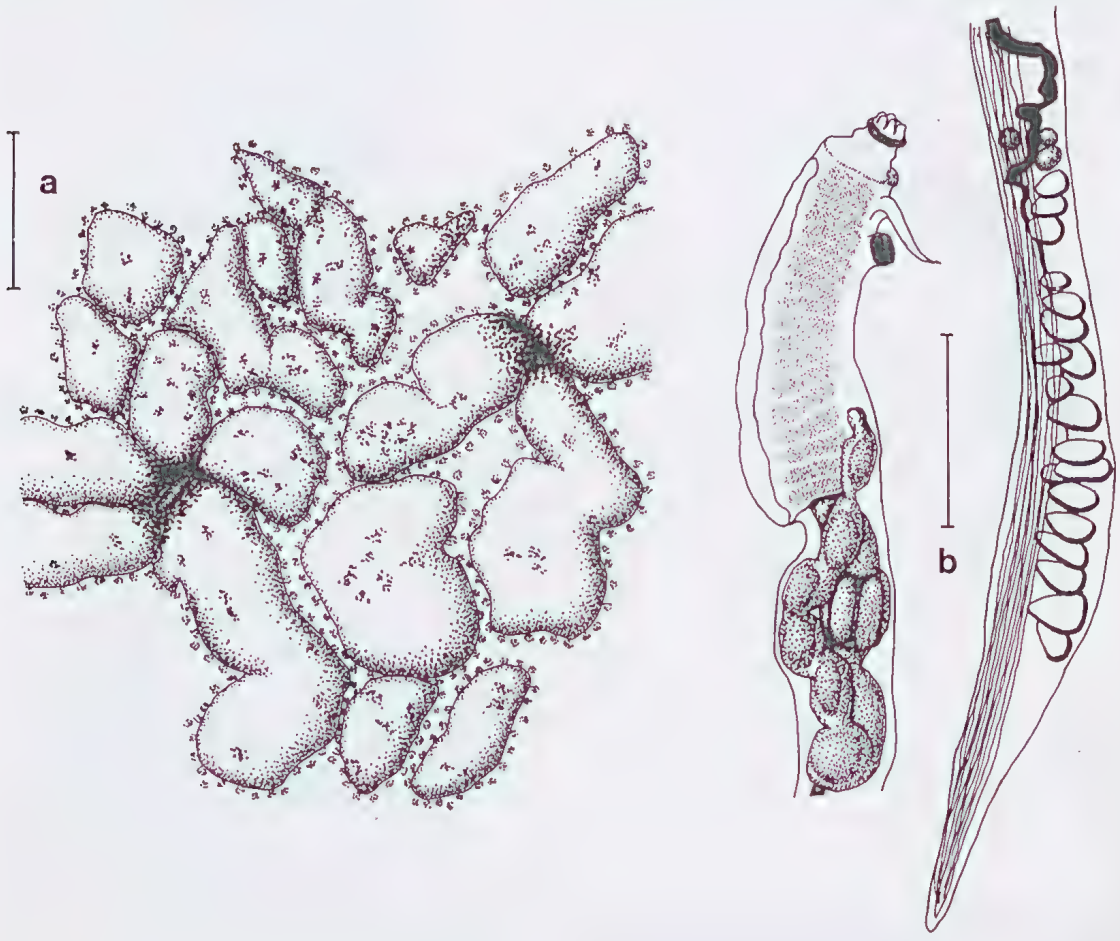


FIG. 84. *Aplidium lenticulum* (paratype QM GH5067) — **a**, part of colony surface; **b**, zooid. Scales: **a**, 5mm; **b**, 1mm.

March). Tailed larvae are in a Heron I. specimen collected in May (QM GH5061). They have median ampullae alternating with the adhesive organs, and a mass of epidermal vesicles obscuring the anterior end of the 1mm trunk. Only one embryo is incubated at a time in the posterior half of the atrial cavity.

REMARKS

As well as the narrow zooids with long thoraces, long branchial apertures and atrial siphons separated from the atrial lip by 3 or 4 rows of stigmata, the gelatinous, flat-topped elevations on the surface, surrounded by the cloacal canals and zooid openings, are characteristic.

The species is the opposite of such species as *A. clivosum* and *A. lunacratum* nom. nov. which, although they have similar zooids, have zooid-free surface elevations of the test that surround the systems rather than being surrounded by the systems as in the present species.

A line of sand outlines the zooid-free areas of test where the branchial apertures open to the surface also in *Aplidium tabascum* n.sp., although in the present species the sand grains in the margins of the elevated areas form a crowded band rather than a single line. Also the cloacal cavities of *A. tabascum* are more extensive, and the atrial lip is from the rim of the aperture and not separate from it as it is in the present species. *Aplidium solidum* has similar, though smaller systems, more embedded sand, and a different zooid.

The surface elevations and similar systems are found also in *A. cellis* Monniot 1987 from New Caledonia but its atrial lip is not separate from the opening, and the larvae of the 2 species differ.

Aplidium caelestis has similar zooids and oval bodies embedded in the surface test as the present species. However its long, crowded meandering systems separated by long, thin ridges, rather than the circular double rows surrounding polygonal areas, and the sandy colonies with surface as well as embedded sand, distinguish it.

The nature and role of the oval bodies is not known, although it is possible that they have sometimes been mistaken for faecal pellets (see *A. caelestis*, above).

Aplidium lodix n.sp.
(Fig. 85)

DISTRIBUTION

TYPE LOCALITY: Victoria (Western Port, Crawfish Rock, coll. J.E. Watson 14.11.78, holoytpe QM G12712).

FURTHER RECORD: South Australia (Perforated I., QM GH4144).

DESCRIPTION

EXTERNAL APPEARANCE: The colony is a large sheet investing pebbles on an irregular substrate. It is uneven in thickness from 0.5 to 1cm. The maximum dimension of the colony is 6cm, and it is irregularly indented and lobed around the margin and smooth and even on the upper surface. The test is firm and translucent, without sand on the upper surface, although there is some on the base. There is no embedded sand. Moderately crowded zooids are arranged in circular to stellate systems. In preservative it is greyish, with whitish zooids.

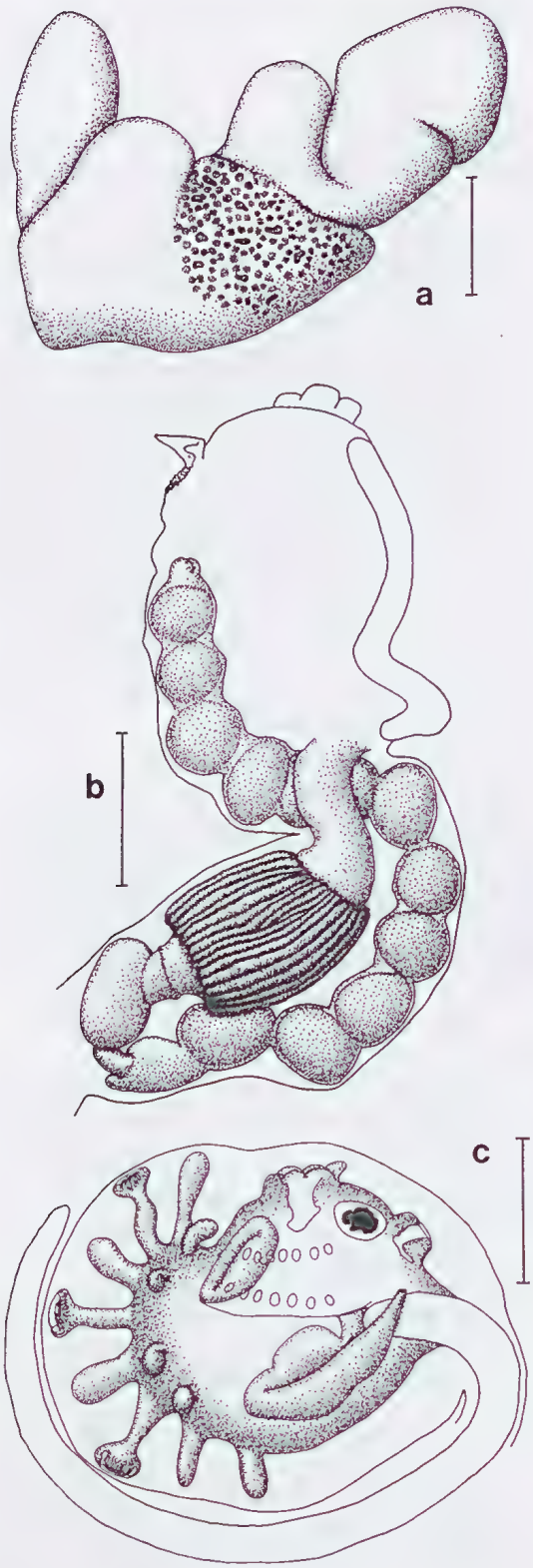
INTERNAL STRUCTURE: Zooids are robust, to 6mm in length, with thorax, abdomen and posterior abdomen each about one third of the total length. The 6 branchial lobes are conspicuous and rounded. The atrial tongue arises from the anterior rim of the aperture. Numerous stigmata are present in 10 rows, although the exact number was impossible to count. The stomach has about 25 longitudinal, parallel folds.

Up to 6 crowded embryos are incubated in the atrial cavity. Larvae from the holotype have trunks 0.65 to 0.75mm long, with the tail wound half-way around. Ocellus and otolith are present. A lateral ampulla is on each side of each of the 4 median ampullae which alternate with the adhesive organs. A ventral median ampulla projects posteriorly, but there are no epidermal vesicles.

REMARKS

Superficially the preserved colony resembles *Aplidium opacum*. However, the latter species has more crowded zooids arranged in double branching rows, and its larva differs from the present species in having epidermal vesicles and lacking lateral ampullae. *Aplidium robustum* n.sp. is another temperate species with a similarly shaped and naked colony, circular systems of varying size, and robust zooids with about 20 stomach folds. It has up to 16 rows of stigmata, its thorax is longer than that of the present species and its larva has clumps of dorsal and ventral vesicles which are not present in *A. lodix*.

Aplidium inflorescens has lateral and median larval ampullae, lacks epidermal vesicles, but is distinguished from the present species by the form of its systems with apical common cloacal apertures.



Aplidium lunacratum nom. nov.
(Fig. 86. Plate 14a-c)

Psammaplidium ordinatum Herdman and Riddell, 1913, p.885. Kott, 1963, p.99.
Not *Psammaplidium ordinatum* Sluiter, 1906, p.22.
Not *Aplidium ordinatum* Sluiter, 1914, p.35. Hartmeyer, 1909–1911, p.1471. Van Name, 1945, p.46.

DISTRIBUTION
NEW RECORDS: Western Australia (Cervantes, WAM 237–9.87); South Australia (Great Australian Bight, SAM E2563; Kangaroo I, QM GH5429; Beachport, QM GH5448; Cape Jaffa, SAM E2553 E2560 E2565, QM GH5446). Victoria (Portland Harbour, MV F59370).
PREVIOUSLY RECORDED: New South Wales (Manning River — AM G12216 holotype *A. ordinatum* Herman and Riddell, 1913).

The discontinuity in the records probably reflects collecting effort.

DESCRIPTION
EXTERNAL APPEARANCE: Colonies are irregular sandy mats, or upright wedges and lamellae up to 1cm thick with zooids opening on both sides, or cylindrical lobes of various sizes arising from common basal test with zooids opening only on the upper surface. Zooids are in evenly spaced circular systems of 5mm diameter. Branchial apertures are in a circle around the periphery of each system and a circular cloacal cavity is in the centre beneath the naked concavities on the surface of the colony. Crowded and relatively large sand grains adhere to the ridges between the systems, and usually to the outside of the conical common cloacal protuberance that rises from the centre of each surface concavity. A little fine sand is embedded in the naked test in the concavity around the base of each cloacal protuberance. Radial bands of red pigment from the cloacal aperture to the circumference of each depression are in the surface test. Sand is crowded throughout the remainder of the test. Zooids lie amongst the embedded sand. They are perpendicular at the surface but more posteriorly they cross one another. In thin lamellae or sheet-like colonies they bend at right angles so that the long narrow posterior abdomina extend through the fine sand in the middle layer of each colony lobe toward its point of fixation, or to where it branches off a

FIG. 85. *Aplidium lodix* n.sp. (holotype G12712) — **a**, colony with systems indicated on part of the surface; **b**, thorax and abdomen; **c**, larva. Scales: **a**, 1cm; **b**, 0.5mm; **c**, 0.2mm.

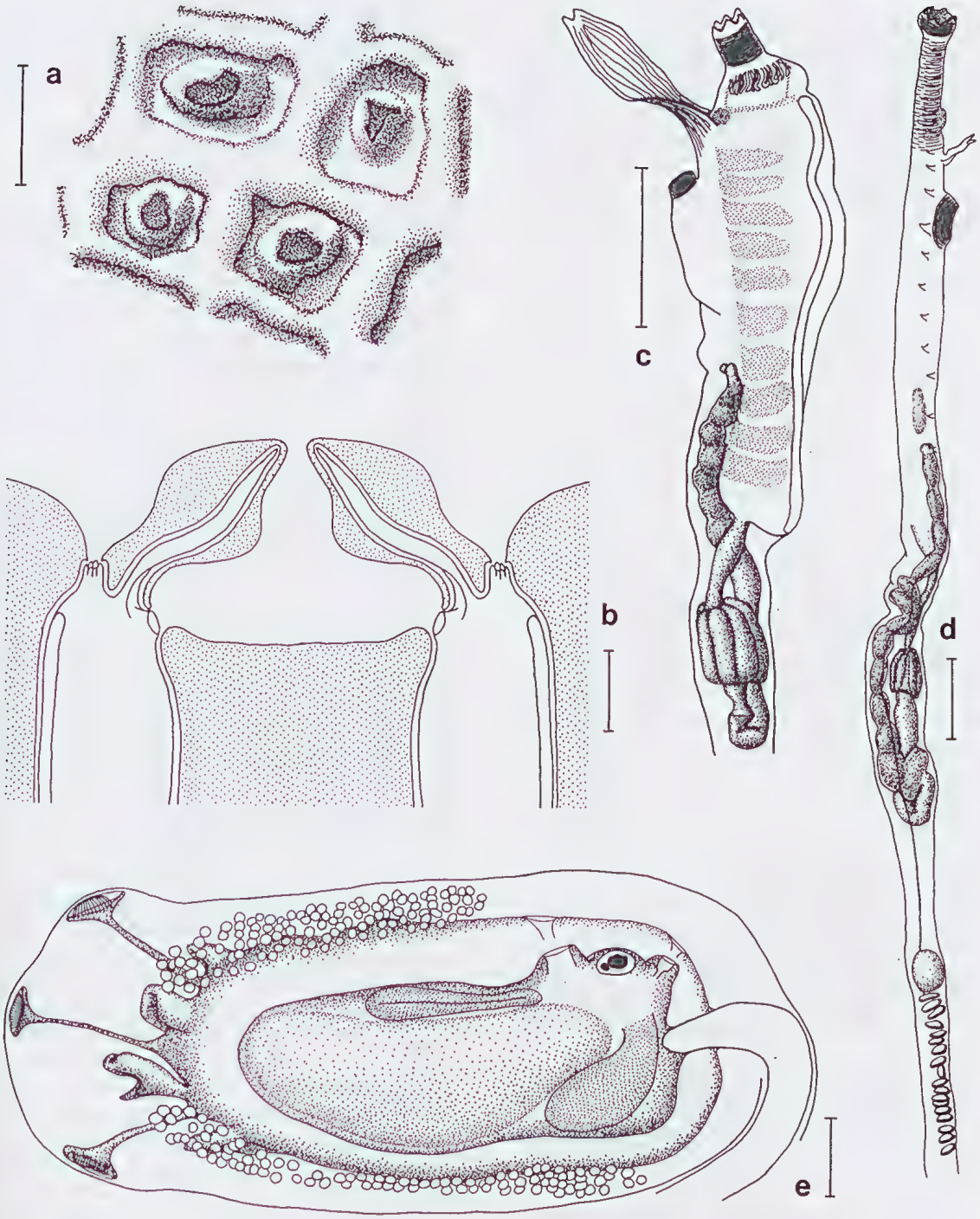


FIG. 86. *Aplidium lunacratum* nom. nov. — **a**, surface of part of colony (QM GH5446); **b**, cross section through the upper part of a zooid system (diagrammatic); **c**, thorax and abdomen (QM GH5429); **d**, extended zooid posterior part of posterior abdomen not shown WAM237.87); **e**, larval trunk (SAM E2563). Scales: **a**, 5mm; **b–d**, 1mm; **e**, 0.2mm.

basal plate. When such lamellae are broken across, the posterior abdomina can sometimes be pulled out in tufts like fine hair-like threads.

INTERNAL STRUCTURE: The zooids are muscular and often are contracted, although the posterior abdomen always is relatively long (up to 1cm or more). When relaxed, the thorax is 3 or 4mm long, and the abdomen about half of that length. Dark pigment cells are in the tip of the atrial siphon and in the branchial siphon of preserved zooids. Longitudinal musculature is strong with about 25 bands on the thorax.

The branchial siphon is short with 6 relatively shallow lobes around the aperture. It has circular muscles in a wide band along its length, and there is no narrow, bulging sphincter muscle. The atrial tongue is fleshy and pointed to long, wide and strap-like, with parallel longitudinal muscles. It arises from the body wall opposite the first row of stigmata, anterior to the atrial siphon which is opposite the second to third rows. A ring of muscles is around the forward pointing atrial aperture on its short siphon which opens into the base of the cloacal cavity around its outer margin. The prebranchial area between the prepharyngeal band and tentacular ring is wide, as is the imperforate pre-stigmatal and post-stigmatal parts of the pharynx. Also a wide band of unperforated pharyngeal wall is along each side of the endostyle.

Stigmata are in 10 to 15 rows of 12 to 15 per row. The stomach is small with 5 shallow folds, sometimes (if the stomach is flattened or inflated) difficult to distinguish and reduced to longitudinal glandular areas internally. The anal opening is opposite the seventh row of stigmata. Spherical to oval male follicles are in a long single or double series in the middle third of the long posterior abdomen. The ovary is just anterior to the testis follicles.

A single embryo is in the posterior half of the atrial cavity of specimens collected in January (SAM E2563). The larval trunk is 2.2mm long, more or less cigar-shaped, with the ocellus and otolith near its posterior end. Two median ampullae, one in each interspace, alternate with the adhesive organs. The anterior end of the trunk is obscured by numerous ectodermal vesicles that extend in bands, one along each side of the ventral and dorsal mid-lines from outside the base of the ventral and dorsal adhesive organs, respectively. The larva is pigmented red and is opaque.

REMARKS

Like *Synoicum castellatum*, the present species has large circular sytems, protruding cloacal apertures, atrial lips separate from the apertures, stomach folds flattened, and occasionally the stomach in the 'atopogaster' condition — with horizontal folds. However the internal glandular areas are all parallel and longitudinal and none are irregular as they are in the large stomach of *S. castellatum*. The present species also has close similarities with other *Aplidium* spp. It has the same long larval trunk (in the vicinity of 2mm) and a long narrow zooid with the atrial lip separate from the opening as in *A. crateriferum* and *A. clivosum* but it lacks their narrow, bulging branchial sphincters, has fewer rows of stigmata, and its systems are smaller. *Aplidium lunacratum* has circular systems (as in *A. crateriferum*) rather than stellate ones (as in *A. clivosum*).

Despite the circular systems of the present species being different from those of the sympatric *A. clivosum*, in which the double rows of zooids converge to the cloacal apertures, preserved colonies are readily confused with one another. Both species have naked surface depressions with central protuberant cloacal apertures and red test. In both the colony shape varies, and variable quantities of sand are on the upper surface. In *A. lunacratum* there seems always to be a single system per depression, as in some specimens of *A. clivosum* (SAM E2564–5). As well as the form of the cloacal systems the present species can be distinguished by its larger zooids, with more muscles, and fewer rows of stigmata but more per row (10 to 14 rows of up to 15). *Aplidium acroporum* has similar systems but smaller zooids, with only 5 rows of stigmata, 8 stomach folds and the atrial lip arising from the anterior rim of the aperture. *Aplidium protectans* has similar circular systems, a large roomy stomach, and larvae with median ampullae and dorsal and ventral vesicles, but its zooids differ in other respects, and its colony is naked and gelatinous.

Examination of the type specimen (AM G12216) of *A. ordinatum* Herdman and Riddell has shown that previous reports (see Kott 1963) of 8 folds in the stomach wall are incorrect. The zooids are contracted, and some of their details are obscured. Nevertheless, the relatively large stomach is seen to have the characteristic 5 shallow folds, the atrial aperture is on a short siphon just posterior to the muscular atrial lip, and each protuberant common cloacal aperture, in the centre of a circle of zooids, has sand embedded in it.

The name *Aplidium ordinatum* is a junior secondary homonym of *Psammaplidium ordinatum* Sluiter, 1906 (see also Van Name 1945) from the Antarctic and the name *Aplidium lunacratum* nom. nov. is accordingly proposed for this species.

Aplidium macrolobatum n.sp.
(Fig. 87)

Aplidium lobatum: Kott, 1963, p.97 (part, colonies from Heron I. and Sarina).

DISTRIBUTION

TYPE LOCALITY: Queensland (Heron I., north east, low tide on under surface or rubble, outer edge of reef, coll. P. Kott 2.11.86, holotype QM GH5169; 14.11.85, paratype QM GH5170).

FURTHER RECORDS: Queensland (Capricorn Group, AM Y1404, QM GH5166–8 GH5219 GH5276 GH5526 GH5544–9 GH5595–6 GH5606–7 GH5660 GH5663; Britomart Reef, QM GH380; Sarina — AM Y1445 Kott 1963; Lizard I., QM GH5550–1).

One colony from Heron I. (QM GH5663) was found on a small crab.

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are investing sheets up to 0.5cm thick, or irregular masses with the upper surface and margin extending into rounded or flattened lobes. Sand is embedded throughout the test, although often it is relatively sparse and the colonies are predominantly gelatinous. Sand is less crowded internally than just below the surface, and is absent from the smooth outer surface of the colony. Branchial apertures on the upper surface have each of the 6 large triangular branchial lobes outlined in fine sand grains. The cloacal apertures are large, sessile or protruding from the surface. They vary in size and shape, some being irregular openings but others regular and circular and often they are particularly extensive long or crescent-shaped openings exposing an extent of the cloacal cavity or canal directly to the exterior.

The systems are either circular, occasionally separated from one another by slight depressions in the surface test (holotype); but in other colonies crowded double rows of zooids converge to irregular and randomly scattered cloacal apertures. In several well developed colonies (QM GH380, AM Y1445) the common cloacal apertures are along the upper rim of flattened colony lobes and double rows of zooids extend down each side of the lobes, almost parallel to one another. The test usually is firm, gelatinous and occasionally glassy in preservative.

In life the colony is cloudy, owing to the embedded sand. When living, the thoracic body walls of the zooids are mauve, purple, raspberry, 'pink', 'hazel', 'rose-red', or 'ruby' (Ridgeway 1886) but other parts of the zooids are colourless. Colonies, with pink or red colour seen through the embedded sand, have been described as 'turkish delight', 'pink lozenge' or 'pomegranate'. Zooids are pale pink in preservative.

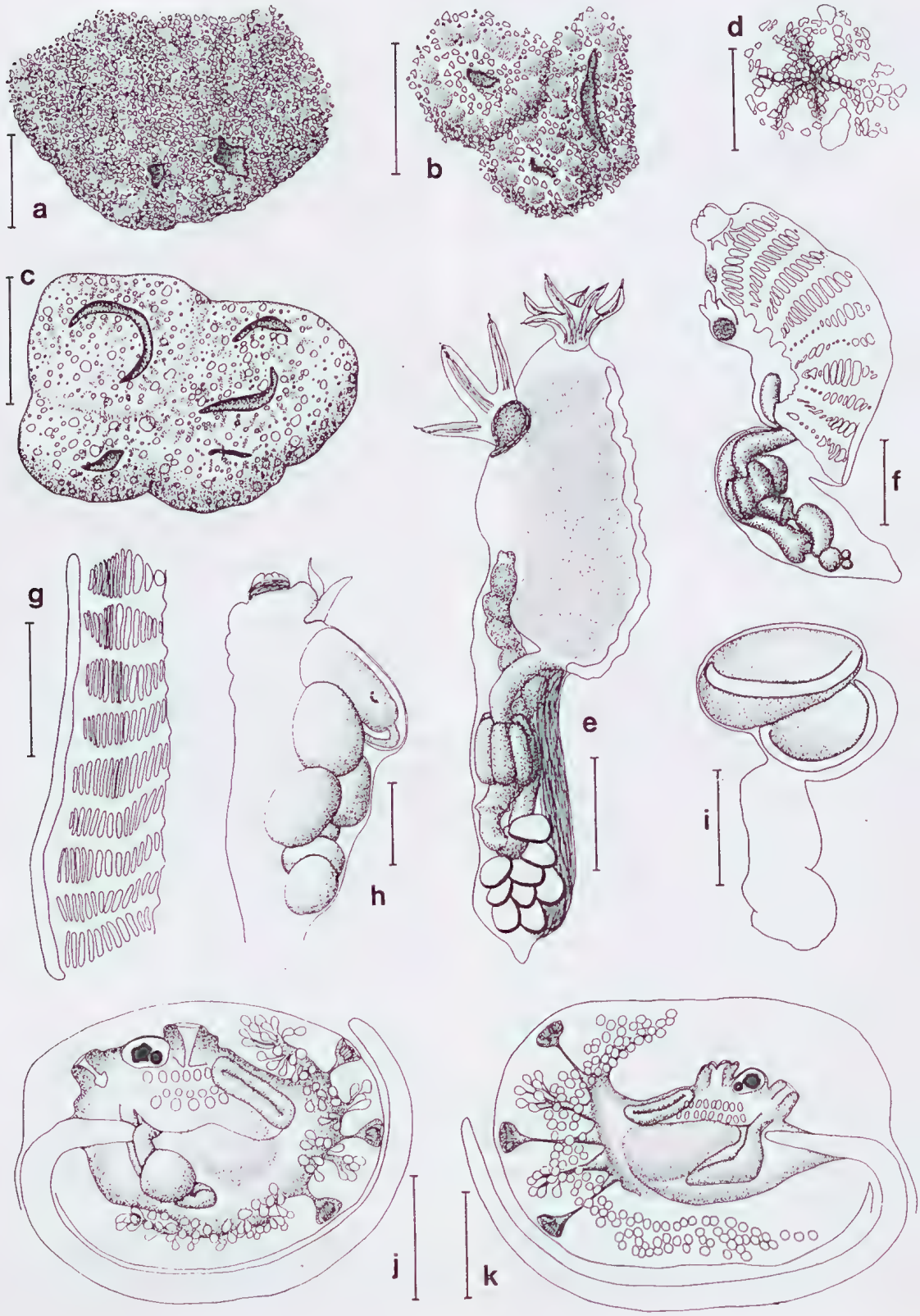
Prochloron is on the surface of some colonies and often large red and green spherical algal cells, 0.1 to 0.2mm in diameter are in the test between and around the zooids and in the floor of the cloacal cavities especially when these are exposed to the exterior (QM GH380 GH5606 GH5660 AM Y1445).

INTERNAL STRUCTURE: Zooids are small, 2mm long when contracted, the thorax and abdomen of about equal length and the posterior abdomen slightly shorter. Branchial lobes are large triangles with a narrow muscle band in the centre of each lobe, reaching to its pointed tip. The atrial lip from the upper rim of the opening is exceptionally large, and is divided into 3 to 5 long, pointed or straight-edged, leaf-like lobes with a narrow strap-like band of muscle fibres in the centre of each lobe. Both atrial and branchial lobes have a similar pointed tip into which the central muscle band is inserted. This tip sometimes appears as a pointed papilla projecting from the end of the lobe. When the muscles in it are contracted it is drawn back into the lobe, subdividing its terminal tip into 2.

Six to 10 strong longitudinal muscles are on the thorax of contracted specimens. These continue along the abdomen and posterior abdomen in 2 strong ventral bands. Nine or 10 rows of up to 15 stigmata per row are in the branchial sac. Stigmata are long and narrow, and are folded up when the delicate thorax is contracted.

The stomach wall has 5 deep folds. Sometimes the posterior abdomen is short, with up to 10 or more pear-shaped male follicles bunched in it. In other zooids, apparently in the female phase, a 3 to 10-egg ovary is about halfway down a long posterior abdomen, possibly after the testis follicles are spent (holotype). Male and female gonads are never present in the one zooid at the same time.

Up to 7 eggs and embryos are packed in the atrial cavity of the holotype and other colonies collected in August and November. The most advanced embryo is anterior. The larval trunk is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0.55 to 0.75mm long, the length increasing with maturity. A well developed ocellus and otolith are in the cerebral vesicle. Clusters of epidermal vesicles branch off the median ampullae that alternate with the 3 small, stalked adhesive organs. A band of small ectodermal vesicles is along each side of the adhesive organs. Further vesicles contrict off from posteriorly projecting stalks part of the way along the dorsal and ventral borders behind the adhesive organs on each side of the median line.

As the larvae mature, zooids degenerate and their remains persist as brood sacs in the test, each incubating one or 2 larvae.

REMARKS

The unusually large and lobed atrial lip, large branchial lobes, red body wall, and short posterior abdomen, with only male or female gonads present at a time, characterise this fleshy species which also contains variable amounts of embedded sand. A similar leaf-like atrial lip is known in the temperate species, *Aplidium elatum* Kott, 1972b. However, the latter species forms upright fan-shaped lamellae, has 8 rows of stigmata with only 8 per row and 15 stomach folds rather than the 5 of the present species. *Aplidium opacum* also has large lobes around the apertures, with muscle bands along the centre of each which sometimes subdivide the branchial lobes and crinkle the edges of the atrial ones. It is distinguished by its more numerous stomach folds and naked colonies without embedded sand.

Aplidium lobatum Savigny, 1816 from the Bay of Suez and Indonesia (see Michaelsen 1920) has a similar number of stigmata, stomach folds and a tripartite atrial tongue from the upper border of the opening. Like the present species, *A. lobatum* has a short posterior abdomen and only the male or female gonad present at one time. However, the colonies of *A. lobatum* have flat-topped oval areas separated by furrows into which the zooids open, and the species does not appear to be conspecific with the present one. *Aplidium tremulum*: Sluiter, 1909, proposed as a junior synonym of *A. lobatum*, has a short atrial lip. Thus, although Michaelsen (1920) may have been wrong in proposing the synonymy of *A. lobatum* and *A. tremulum* apparently neither are conspecific with the present species.

The degenerate zooids acting as brood pouches in the test, appear to be characteristic of the present species.

Aplidium magnilarvum n.sp.
(Fig. 88)

DISTRIBUTION

TYPE LOCALITY: Western Australia (115 nautical mls SW Eucla 38°17'S, 129°37'E, 180m, coll. W. Zeidler and K. Gowlett Holmes 16.1.89, holotype SAM E2582, paratype SAM E2583).

FURTHER RECORD: Western Australia (SSW Eucla, SAM E2590).

The species has been taken from the same general area at 180 to 190m depth.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are hard, upright, round-topped, about 4cm high and 2-3cm maximum diameter, narrowing toward the base where an aggregate of root-like projections of the test form a holdfast. Sand is not so crowded internally as it is on the surface around the sides and roots of the colony where it adheres to the test to form a thick layer. The sand layer is thinner toward the upper surface.

The surface sand obscures the systems, and their form was not determined. In between the sand particles, the test is firm and glassy, sometimes with some brown pigment cells.

INTERNAL STRUCTURE: The zooids in the availabile material are entering the vegetative phase with trophocytes accumulating in the abdomen, and the thoraces disintegrating. Only in the holotype are there adult organs persisting in the zooids. In some of these zooids a single large embryo is incubated in the atrial cavity, although none of these appears to have any larval organs developed.

In these zooids, the thorax (contracted) and abdomen together are up to 4mm. The thorax is muscular with about 15 longitudinal muscles running the length of the zooid, forming a wide band along the ventral border of the abdomen and posterior abdomen. The circular atrial aperture is

FIG. 87. *Aplidium macrolobatum* n.sp. — **a**, colony (QM GH5545); **b**, upper surface showing circular systems and large, irregular, sessile cloacal apertures (holotype QM GH5169); **c**, upper surface showing elongate systems with long, open cloacal apertures and embedded symbionts (QM GH5606); **d**, showing branchial lobes outlined in sand grains (QM GH5167); **e**, **f**, zooids showing short, contracted posterior abdomina with testis follicles and oocytes respectively (QM GH5167, holotype GH5169); **g**, portion of branchial sac (QM GH5314); **h**, thorax showing embryos being incubated (holotype QM GH5169); **i**, embryo being brooded in thorax of degenerating zooid (QM GH5526); **j**, **k**, larvae (QM GH5315). Scales: **a–c**, 5mm; **d–i**, 0.5mm; **j**, **k**, 0.2mm.

antero-dorsal, directed anteriorly, with a muscular atrial lip arising from the body wall just in front of it. The atrial lip either is undivided or it has 2 additional points on each side of the longer median one.

Stigmata are in 21 long rows. The thoraces are wide and robust, and appear to have at least 20 stigmata per row, although the exact number was not determined. The oesophagus is relatively long, and the long elliptical prestomach occupies most of its length. The stomach is short and has 5 deep folds. The post pyloric part of the gut has a posterior stomach, and proximal and distal parts of the mid-intestine. There are short rectal caeca. The gut is narrow in these specimens, however, and probably is not functional.

The large embryo completely filling the atrial cavity in some of the holotype zooids is up to 2mm long.

REMARKS

These small, upright bulbous colonies, with their basal holdfasts are unique, distinguished from *A. coniferum* by their hard, sandy consistency, the single large embryo in the atrial cavity, and more numerous stigmata in each row. This new species may be confined to locations at more than 100m depth on the southern continental shelf.

Aplidium minisculum n.sp.
(Fig. 89a,b)

Aplidium depressum: Kott 1976, p.60.

DISTRIBUTION

TYPE LOCALITY: Victoria (Portsea Pier, 2m, Panel 7-2 coll. G. Russ 24.2.76, holotype QM G11920).

FURTHER RECORD: Victoria (Westernport — Kott 1976).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are soft, jelly-like flat-topped cushions to more extensive sheets lobed on the upper surface. They are found on stalks and fronds of weed. The holotype is from an experimental fouling panel. Zooids are in circular to elongate systems, and are clearly seen through the transparent but slightly brownish test. Their arrangement often is obscure in preserved

FIG. 88. *Aplidium magnilarvum* n.sp. — **a**, **b**, colonies (holotype SAM E2582, E2590); **c**, thorax and abdomen showing embryo being incubated in atrial cavity (SAM E2590). Scales: **a**, **b**, 1cm; **c**, 0.5mm.

material. Sand particles are embedded in the test, but are not crowded.

INTERNAL STRUCTURE: Zooids are small, to about 3mm, of which the thorax and abdomen are about half. The small, terminal branchial aperture has 6 pointed lobes, and the small atrial aperture has a single, short, pointed lip projecting out from the upper rim of the opening. Five rows of 10 to 12 stigmata are in the pharynx. The gut loop is short, with a small stomach with 10 deep folds in its wall. An oval posterior stomach is at the posterior end of the descending limb of the gut loop. A large rectal valve is present at the junction of the mid-intestine and rectum (at the base of the

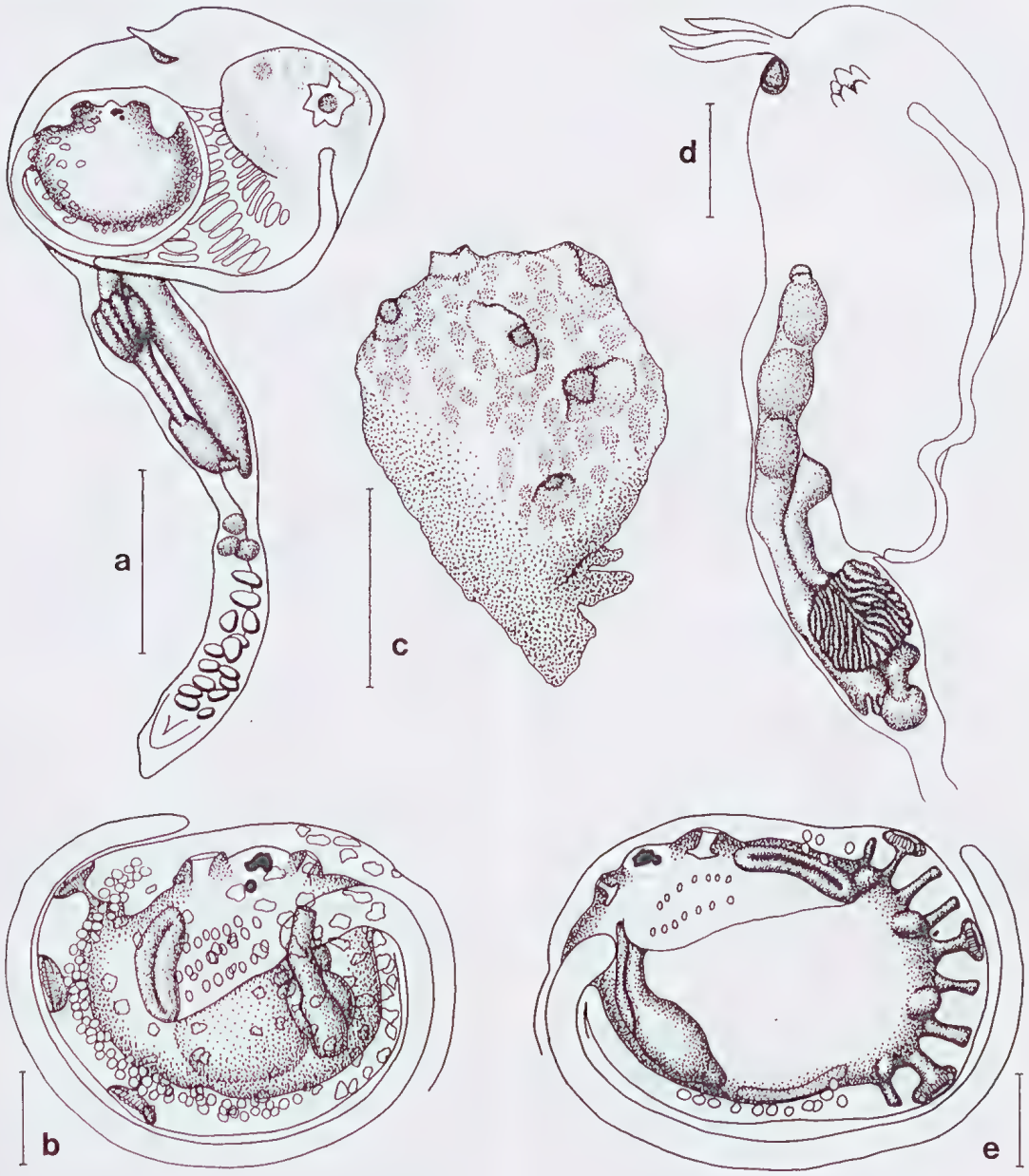


FIG. 89.*Aplidium minisculum* n.sp (holotype QM G11920)—**a**, zooid with embryo in atrial cavity; **b**, larva *Aplidium multilineatum* n.sp. — **c**, colony (holotype AM U3954); **d**, zooid (holotype AM U3954); **e**, larva (*A. flavolineatum*: Kott 1963 Cape Vlamingh, Rottnest I.). Scales: **a, d**, 0.5mm; **b**, 0.1mm; **c**, 5mm; **e**, 0.2mm.

ascending limb of the gut loop). The short posterior abdomen has a 2 or 3 egg ovary anterior to an irregular double row of male follicles.

In the holotype colony a single larva is in the atrial cavity, causing the short thorax to be almost spherical. These zooids also have mature male follicles, sperm in the vas deferens and some small oocytes in the ovary.

Larvae are almost spherical with a double row of ectodermal vesicles along each side of the median short-stalked adhesive organs, 3 rows of stigmata and large conspicuous test cells in the larval test. These test cells are absent from the anterior end of the larval trunk and become more crowded posteriorly. The larval trunk is about 0.4mm long.

REMARKS

Kott (1976) assigned the specimens from Westernport Bay to *A. depressum* on the basis of their similar colonies, small zooids, and similar numbers of rows of stigmata, numbers per row and numbers of stomach folds. Although there are similar test cells in the larval test, the larvae of *A. depressum* are smaller than those of the present species and have only a single row of 7 or 8 vesicles along each side of the adhesive organs. The zooids of *A. minisculum* also differ from those of *A. depressum* in the presence of an atrial lip.

Aplidium multilineatum n.sp.
(Fig. 89c–e)

Aplidium flavolineatum: Kott, 1963, p. 5 (part, AM U3954, ? AM U3955).

DISTRIBUTION

TYPE LOCALITY: Western Australia (Rottnest I., Salmon Bay, inner pool, low tide, coll. P. Kott 18.11.51, holotype AM U3954).

FURTHER RECORDS: Western Australia (? Cape Vlamingh, Rottnest I. — Kott 1963). ? Tasmania (Hunter I. — AM U3955 Kott 1963).

DESCRIPTION

EXTERNAL APPEARANCE: The colony is a flat-topped cushion, 1cm in diameter, with a naked upper surface and a sandy base. Some sand is embedded in the test around the zooids but it is sparse, and is absent altogether from the surface test in the centre of the circular systems of zooids where large, plain-rimmed common cloacal openings protrude from the surface. The systems are numerous, about 8 being present in the small holotype. The test is soft and transparent in the preserved colony.

INTERNAL STRUCTURE: Zooids are delicate, with a large thorax twice the length of the abdomen and broader as well. The posterior abdomen is long and narrow. Fine longitudinal muscles are on the thorax. An atrial lip divided into 2 or 3 narrow, pointed branches, arises from the anterior rim of the antero-dorsal atrial aperture. Stigmata are in 10 rows of up to 16. The stomach is small with about 30 narrow, mostly oblique folds that are interrupted where they meet along lateral, mesial, dorsal, and ventral longitudinal lines which divide the stomach wall into 4 sections. The usual duodenum, mid-intestine and posterior stomach are in the descending limb of the gut loop. A rectal valve is at the proximal end of the rectum.

Embryos are not present in the holotype. Slide-mounted larvae are available from colonies from Cape Vlamingh (Rottnest I.) and Hunter I. (Tasmania). These were from colonies which, with the present colony, were assigned to *A. flavolineatum* by Kott (1963). The colony from Hunter I. (AM U3955) appears to have dried out at some time and neither the systems nor the structure of the zooids could be discerned. The specimen from Cape Vlamingh has not been located for reexamination. Thus the identity of these larvae cannot be confirmed, and they are only provisionally assigned to the present species — on the assumption that colonies from which they were taken were conspecific with the reexamined colony, viz. the holotype of the present species.

The larvae from both Hunter I. and Cape Vlamingh have a trunk 0.9mm long, with the tail wound about three-quarters of the way around it. There are median ampullae alternating with the adhesive organs, and those in the 2 interspaces are each divided into 2. Four lateral ampullae are present on each side of the median line, one near the base of each of the median ones. A trail of epidermal vesicles extends posteriorly from behind the dorsal and ventral median ampullae. A large ocellus and an otolith are in the cerebral vesicle.

REMARKS

The cushion-like colony with transparent test, and circular systems has some resemblance to *Aplidium uteute*, although the zooids and the systems appear larger, and the common cloacal apertures more protuberant. *Aplidium uteute* also has numerous stomach folds, but they are longitudinal rather than oblique, and it has a wide

thorax with more stigmata than the present species. Larvae of *A. uteute* with single series of epidermal vesicles around each side of the median line, and vesicles between the adhesive organs, are completely different from the larvae provisionally assigned to the present species.

Aplidium gastrolineatum has circular systems and oblique stomach folds but the stomach folds are fewer than in the present species, and the thorax is longer with about 16 rows of stigmata. The South African species *A. flavolineatum*, to which the holotype of the present species was assigned by Kott (1963), has a similar number of stomach folds, but they are not oblique.

The larvae provisionally assigned to the present species have median and lateral ampullae and dorsal and ventral vesicles like those of *A. robustum* and *A. ornatum*, but the median ones are subdivided and there are 4 lateral ones rather than only 2 (as in the latter 2 species). *Aplidium robustum* has a similar colony, but sessile cloacal apertures and fewer stomach folds.

Aplidium multiplicatum Sluiter, 1909
(Fig. 90. Plate 14c–f)

Aplidium multiplicatum Sluiter, 1909, p.101. Tokioka, 1967, p.35 (part). Kott and Goodbody, 1982, p.514.
Amaroucium multiplicatum: Van Name, 1918, p.165. Nishikawa, 1984a, p.112.
Not *Aplidium multiplicatum*: Millar, 1963, p.693 (>?). Kott 1963, p.103.
Not *Amaroucium multiplicatum*: Tokioka 1953, p.180. Nishikawa and Tokioka, 1976, p.379. Nishikawa, 1990, p.89.
Aplidium opacum Kott, 1963, p.108 (part, from NSW and SW Australia).
Aplidium flavolineatum: Kott, 1963, p.105 (part, specimens from NSW and AM U3956 from Rottnest I.); 1972c, p.246.
Aplidium californicum: Monniot, 1987, p.518.
? *Aplidium multiplicatum*: Renganathum and Monniot, 1982, p.259.

DISTRIBUTION

NEW RECORDS: Northern Territory (Darwin Hbr., QM GH5361). Western Australia (Cockburn Sound, WAM 46.72 22.75 29.75 143.75 227.82). South Australia (Yorke Peninsula, SAM E2540 E2587; St Vincent Gulf, SAM E2594). New South Wales (Port Hacking QM GH31).Queensland (Capricorn Group, QM GH1359 GH5108–27 GH5470 GH5218 GH5224 GH5241–2 GH5275 GH5281 GH5532–8 GH5540–1 GH5646; Whitsunday Is, QM GH5366; Lizard I., QM GH5539; far northern Great Barrier Reef, QM GH5337).

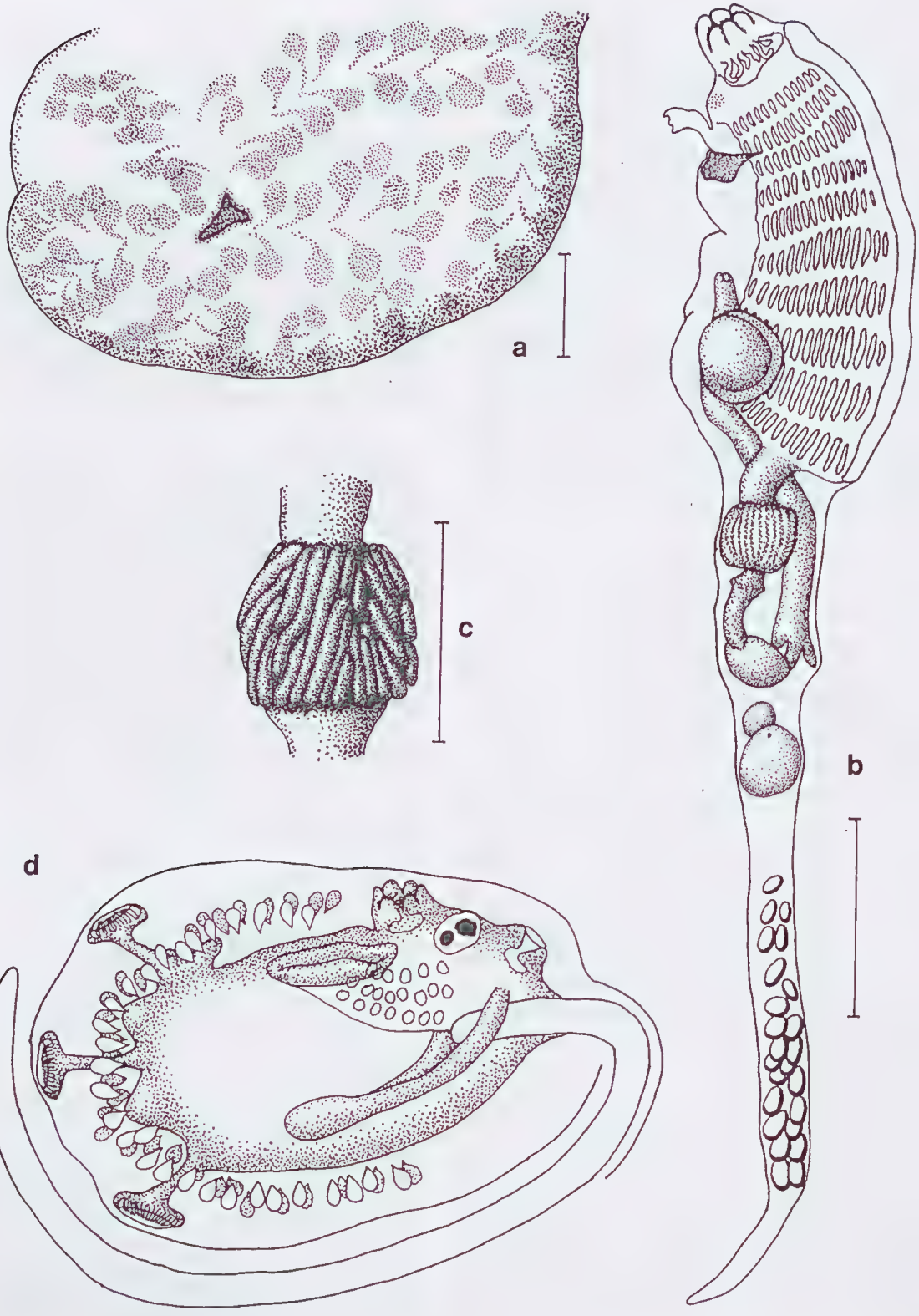
PREVIOUSLY RECORDED: Western Australia (South-western — AM Y1394 Kott 1963). New South Wales (Jervis Bay — AM Y1439; Port Hacking — AM Y815 Y823 Kott 1972c; Port Jackson — AM Y1423 U3931 U3956 Kott 1963). Kiribati and the Palau Is (Tokioka 1967); Phillipines (Van Name 1918); Truk and Ponape Is, Majuro Atoll (Nishikawa 1984a). Hong Kong (Kott and Goodbody 1982).

Despite confusion in the definition of this species which resulted in its being placed in synonymy with eastern Pacific and S. African species, the range appears to be Indo-West Pacific. It is especially common in tropical, usually reefal, habitats of the western Pacific. It extends into the temperate waters of south-western Australia, but not across the southern coast of the continent.

DESCRIPTION

EXTERNAL APPEARANCE: The species forms cushion- or plate-to spreading sheet-like colonies, to 7cm in maximum dimension and 1cm thick, with irregular borders. The upper surface is often even and horizontal. A colony from the Great Barrier Reef (QM GH5470) is a glassy dome, 6cm high, with the surface deeply divided into lobes of varying size and shape; and the specimen from Darwin Harbour (QM GH5361) has the upper surface raised into high, zooid-free round ridges between the double rows of zooids. In other parts of the colony, however, systems are more crowded. Zooids are crowded, along each side of canals that converge to a few large, sessile common cloacal apertures with irregular borders. The living specimens have translucent, slightly cloudy test coloured orange, pale apricot, 'poppy red', 'salmon' 'pinkish buff', 'yellow-buff', 'cream-buff' (Ridgeway, 1886). Zooids are crimson, 'scarlet vermilion', 'geranium red', 'scarlet', 'ruby', 'coral reef' (Ridgeway *loc. cit.*) brilliant or bright orange, or pink. When embryos are present they are a dark maroon colour. In preservative the test is translucent but cloudy, cream with pink zooids and mature eggs and embryos (but not tailed larvae) are a translucent brownish colour. Opaque white (possibly blood) cells are in the sheath of soft test around the zooids, and are crowded together to form a white band around the branchial siphon. The test is particularly soft, jelly-like, is easily torn, and the surface is smooth.

In some colonies green *Prochloron* cells and diatoms are in the common cloacal cavity, in the canals converging to them and on the outer surface of the colony. The species is one of the 5 or


a
b
c
d

6 *Aplidium* spp. which sometimes have *Prochloron* in the cloacal cavity (see Kott *et al.* 1984: *Aplidium* sp.3).

INTERNAL STRUCTURE: Zooids are small, the contracted thorax and abdomen together being about 2mm long. The posterior abdomen is short (about one-third of the total zooid length). The opaque white corpuscles that are such a feature of this species are in the body wall of the pharynx and atrial lip as well as around the base of the branchial siphon, and in the test around the zooid. The body wall is delicate with about 12 fine longitudinal muscle bands. Transverse muscle fibres are in the transverse vessels betwen the rows of stigmata.

The 6 branchial lobes are variable, but they usually are long, and are either pointed or rounded. The atrial lip, from the upper rim of the opening contains longitudinal muscles and is of various lengths. Its tip either is pointed and undivided, or is divided into 3 or 4 separate points. There are 9 to 11 rows of 14 to 20 stigmata. Twenty-two longitudinal folds are in the wall of the small stomach which is about halfway down the abdomen. The stomach folds are sometimes irregular, interrupted, and slightly oblique on the outside or ventral border of the stomach, but elsewhere they are longitudinal and parallel.

Bunched testis follicles occupy about three-quarters of the length, of the posterior abdomen, leaving the anterior quarter free of male follicles. In relaxed zooids the follicles are spread out into 2 irregular rows. A small ovary is behind the gut loop, anterior to the testis. Up to 2 embryos are in the atrial cavity of zooids collected in August from Darwin, May from the northern Great Barrier Reef, October from the Whitsunday Is, and January, April, May, August, October and November from the Capricorn Group. Some specimens from Port Hacking (AM Y815) have up to 7 embryos packed into the atrial cavity of specimens collected in June. When zooids are particularly contracted the embryos project out from the body wall in what could be mistaken for a brood pouch. The larval trunk is up to 0.9mm long, and the tail is wound about two-thirds of the distance around it. On each side of the 3 median adhesive organs, is a single arc of up to 30 large epidermal vesicles. Small conical median ampullae alternate with the adhesive organs in all except some of the smaller (0.6 to 0.7mm long trunk) and almost spherical larvae from the Capricorn Group, which also have fewer (14 to 20 rather than 20 to 30) epidermal vesicles in each lateral arc. The same opaque white corpuscles are in the larval test as those in the test sheath around the zooids, and in a band around the branchial siphon. These sometimes obscure the larval organs, especially those at the anterior end of the trunk.

REMARKS

The characteristic of this species are the opaque white corpuscles clustered around the branchial siphon and the zooid, and scattered in the cloudy, soft gelatinous test, as well as long, double row systems, numerous stomach folds, the moderately wide thoraces (with up to 16 stigmata per row), and larvae with lateral arcs of numerous (14 to 30) epidermal vesicles.

The discrepancy in larval size, and in the number of epidermal vesicles, between smaller almost spherical larvae from the Capricorn Group and the larger ones from the same as well as all other locations is puzzling. The only other difference observed is in the size (and probably the age) of the colonies. These Capricorn Group specimens, taken at low tide from rubble near the edge of the reef, are smaller than the colonies taken from other locations by SCUBA divers.

Sluiter's type specimens of *A. multiplicatum* are irregularly lobed plates 3cm in maximum diameter and 5 to 6mm thick, glassy and transparent, with the yellowish-white zooids showing through the test. Systems were not identified. Sluiter records delicate muscles, 7 rows of 10 stigmata, 18 longitudinal stomach folds and a short posterior abdomen with bunched male follicles.

Van Name (1918) reported larger specimens from the Philippines with more complex systems and 7 to 10 rows of up to 16 stigmata per row, with the same number of stomach folds (18–20) and double series of testis follicles. As in specimens of this and other species, the arrangement of the gonads and the length of the posterior abdomen changes with development of the zooid and with its state of contraction.

Aplidium multiplicatum: Kott, 1963 came from 2 locations in Queensland. Zooids from both locations are smaller than those of *A. multiplicatum* with only 6 or 7 rows of stigmata. Colonies from Sarina (AM Y1448) are specimens of *Aplidium fluorescum*. The colonies from Currumbin (AM U3994), with a layer of sand on the surface,

FIG. 90. *Aplidium multiplicatum* — **a**, part of small colony, indicating zooids along each side of the cloacal canals which converge to the common cloacal apertures (QM GH5113); **b**, zooid (QM GH5110); **c**, stomach, showing interrupted folds; **d**, larva (QM GH5361). Scales: **a**, 2mm; **b**, 1mm; **c**, 0.5mm; **d**, 0.2mm.

appear to be colonies of *A. ornatum* with circular systems and sand around the margin of the colony. *Aplidium multiplicatum*: Millar, 1963 is also wrongly assigned. The 3 specimens have circular systems, about 25 stigmata per row and 21 stomach folds. The larvae have lateral ampullae but no vesicles. It is possible that more than one species is involved. The number of rows of stigmata and number per row suggest *A. uteute* is one of the species, but the larvae and the number of stomach folds do not support that view.

Specimens assigned to *A. multiplicatum* by Tokioka (1967) also may include more than one species. In specimens only 2.0cm in maximum dimension, and not more than 1cm thick, there are some with circular, and others with more complex systems, a range of colours from 'pale brown', 'reddish brown', to 'purplish brown' (Tokioka 1967), 7 to 10 rows of stigmata, 10 stigmata per row (in zooids from Kiribati) up to 30 (larger zooids from Palau Is), and 20 to 35 stomach folds. The range in these characters is greater than could be regarded as intraspecific variation and greater than could be regarded as the effects of growth, especially when the range in colony size is relatively small. The larvae of the small colony from Kiribati, and the zooids figured from both Kiribati and the Palau Is (Tokioka 1967, Figs 8a–d, 9a,b) appear to be *A. multiplicatum*. Colonies with more numerous stigmata and stomach folds could be other species such as *A. uteute*, which resembles the present species in the colour of its zooids and embryos. However, *A. uteute* has median as well as lateral larval epidermal vesicles, more stigmata in each row and more stomach folds than *A. multiplicatum*.

Nishikawa and Tokioka (1976), Nishikawa (1990), Tokioka (1953) and Rho (1975) have assigned specimens from Japanese waters with 7 to 11 rows of stigmata, and 20 to 25 stomach folds to *A. multiplicatum*. The number of stigmata per row, and the arrangement of larval epidermal vesicles and ampullae do not fall within the ranges recorded for the present western Pacific species.

Tokioka (1953, 1967) proposed that the eastern Pacific *Aplidium californicum* (Ritter and Forsyth, 1917) is a synonym of the present species. However, the Californian species has sand embedded in the test, an atrial lip separate from the opening, fewer stigmata per row, and lacks the characteristics pigmentation of the present species (see Kott and Goodbody 1982, Nakauchi 1987, Millar 1988). *Aplidium californicum*: Monniot, 1987 from New Caledonia has the characteristic naked colony, pigmentation, stomach wall, branchial sac and larval form of *A. multiplicatum*.

In Australia *Aplidium opacum* is the species most closely related to the present one and specimens have been confused. It has similar colonies with crowded zooids in long branching double-row systems. Zooids are sheathed in a layer of soft test containing opaque white cells which are similar to those in *A. multiplicatum*, and are crowded around the branchial siphon in much the same way. The zooids also are similar, although the present species usually has more stigmata per row but fewer rows than *A. opacum*. *Aplidium opacum* has firmer test, and the larvae have long finger-like median ampullae that project between the adhesive organs, as well as a band of numerous lateral vesicles (rather than the single series arc that occurs in *A. multiplicatum*). Re-examination of some of the specimens from New South Wales and south-western Australia assigned to *A. opacum* by Kott (1963) has shown them to belong to the present species. Larvae of the south-western Australian specimen are characteristic of *A. multiplicatum* (see Kott 1963, p.110, Fig. 22). The ranges of *A. multiplicatum* and *A. opacum* overlap on the eastern and western coast, but the former is not recorded from southern Australia, and the latter species does not extend into the tropics (see *A. opacum*, below).

Kott (1963) wrongly assigned colonies of the present species and others (viz. *A. gastrolineatum*, *A. multilineatum* and *A. robustum* n.sp.) to the S. African *A. flavolineatum*.

Aplidium opacum Kott, 1963
(Fig. 91. Plate 15a–c)

Aplidium opacum Kott 1963, p.108 (part, holotype AM U3929).
Aplidium pliciferum: Kott, 1963, p.106; 1972a, p.13; 1976, p.62.
Aplidium foliorum Kott, 1975, p.5.

DISTRIBUTION
NEW RECORDS: Western Australia (Rockingham, QM GH5461). South Australia (Great Australian Bight, SAM E2591; Port Bonython, QM GH4234–6, Perforated I., QM GH4194; Spencer Gulf, QM GH5440–1; Yorke Peninsula, SAM E2540 E2571 E2587; St. Vincent Gulf, SAM E2484 E2586 E2594). Tasmania (SE Fluted Cape, SAM E2589). New South Wales (Port Hacking, QM GH31).
PREVIOUSLY RECORDED: South Australia (Great Australian Bight — Kott 1975; St. Vincent Gulf — Kott

1972a). Victoria (Balnarring Beach — AM U3929 holotype Kott 1963; Westernport — Kott 1976).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are large and fleshy sometimes almost spherical or flattened upright masses to 8cm high and 6cm diameter. More often they are flat-topped, extensive cushions often with the surface partly divided. Crowded zooids are perpendicular to the surface, but posteriorly criss-cross one another in the test.

In preservative the test is soft, but firm, gelatinous and translucent white with minute opaque cells, possibly blood corpuscles, in a soft layer of test that sheaths each zooid. These opaque cells are especially crowded around each branchial aperture.

In photographs of well-developed living colonies zooids are seen to be in crowded, branching double rows, with large branching primary cloacal canals separating areas packed with zooids and secondary cloacal canals. Large, sessile common cloacal apertures are scattered over the surface at the junction of the primary canals. Zooids are cream (QM GH5441) or pink (QM GH5440). One colony (QM GH4194) is described as an 'orange morph'; and one is bright yellow (SAM E2586). At least 2 colour variants occur, both translucent, one pink or orange and one yellow or yellowish cream.

INTERNAL STRUCTURE: Zooids are relatively long and robust. The thorax and abdomen even when contracted are together up to 5mm long and the posterior abdomen is from twice to many times that length. About 15 strong longitudinal muscle bands extend from the thorax to the posterior end of the abdomen. The branchial siphon is short, often with well-developed bifid lobes. The atrial aperture, beside the third row of stigmata, has a fleshy muscular atrial lip, usually deeply divided into 3 equal, pointed lobes, from the upper border of the opening. Muscles are along the centre of each lobe, and when these are contracted the lobes are frilled and crinkled along the edges. The atrial lip is often (but not always) large and conspicuous.

Stigmata are in 12 rows with up to 12 in each row. The stomach is of moderate length with 20 narrow, sometimes interrupted folds. The thick duodenum, mid-intestine and oval posterior

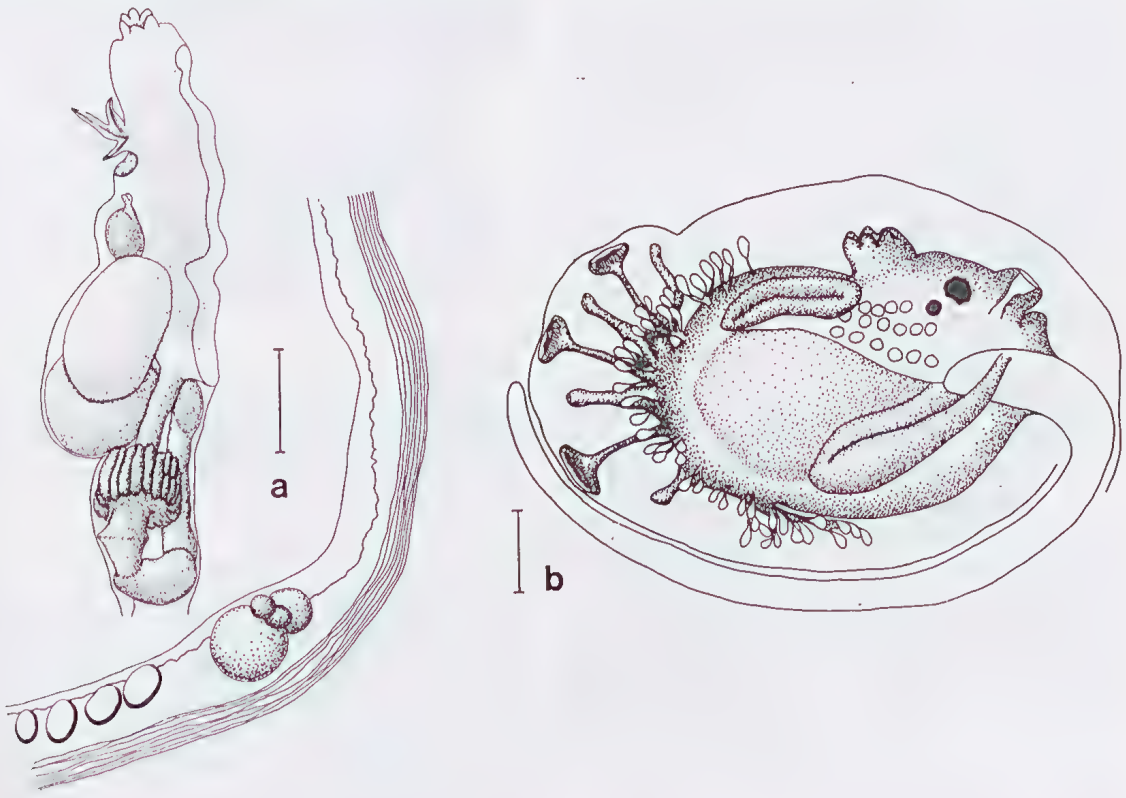


FIG. 91. *Aplidium opacum* — **a**, zooid, showing anterior part of posterior abdomen and embryos being incubated (QM GH5441); **b**, larva (QM GH4234). Scales: **a**, 0.5mm; **b**, 0.1mm.

stomach are characteristic of the genus, and there are 2 pronounced rectal caeca. Gonads are in the posterior part, or the whole of the narrow posterior abdomen, with the small ovary anterior to the long double series of male follicles.

One to 3 embryos are incubated in the top of the abdomen and in the atrial cavity, but only one at a time develops to a tailed larva. They are present in specimens from South Australia collected in February (QM GH5441 GH4234 SAM E2586), April (QM GH4236 GH4194), May (QM GH4235) and November (SAM E2571). Larvae have a trunk about 0.7mm long and a sturdy tail reaching to the anterior end of the trunk. Ectodermal vesicles (about 35) are crowded in an arc along each side of the adhesive organs. These vesicles are not in a single series, and clumps of them branch off a single stem from the larval ectoderm. Narrow, pointed, median ampullae alternate with the adhesive organs.

Remarks

Both the zooids and the large gelatinous colonies, with randomly scattered, sessile common cloacal apertures, and crowded branching systems of zooids in the present species are similar to *Aplidium multiplicatum*. These species also have in common the cloudy opaque cells in a sheath of soft test around each zooid, and about 20 stomach folds. The zooids of *A. opacum* are larger than those of *A. multiplicatum* however, and although they have the white opaque cells in a sheath around the zooids, they do not form as wide a band around the branchial aperture as in *A. multiplicatum*. The branchial sac of the present species is relatively narrower than that of *A. multiplicatum*, which has up to 20 stigmata per row but fewer than 12 rows. Larvae differ from those of *A. multiplicatum*, having long median ampullae and clumps of lateral vesicles in lateral bands (rather than a single arc of vesicles on each side).

Kott (1963) assigned several colonies to this species which have subsequently been found not conspecific with the holotype. A colony from Balnarring Beach (AM Y1401) made up of several lobes joined to a common base is probably a specimen of *A. inflorescens* (see above). The colonies from western Australia and Port Jackson (AM Y1423 Y1439) are specimens of *A. multiplicatum* as is the larva figured by Kott (1963, Fig. 22). Colonies from Tasmania with zooids in which the atrial aperture is separate from the atrial lip are also erroneously assigned to this species and appear to be colonies of a *Polyclinum* sp.

Kott (1963) assigned specimens of the present species from Cockburn Sound to *Aplidium plicif-erum* (Redikorzev, 1927). The latter species, known from coastal waters of Japan, including the Inland Sea (Tokioka 1953), has large colonies with branching double row cloacal systems as in the present species, and zooids and larvae which also appear to be similar to the Australian species. Only the stomachs are different, having from 25 to 32 fine pleats in the Japanese species, while the Australian one has 20 to 24. Thus the number of stomach folds appears to be the principal character separating these species, which are indigenous to temperate Australian and Japanese waters respectively. Despite their resemblance to one another, they apparently have different geographic ranges, and are separated from one another by the tropics.

Aplidium foliorum Kott, 1975 was thought to be distinguished by its large tripartite atrial lip. An identical lip now is known to be characteristic of the present species, although its length varies to some extent according to the position of the zooids relative to the cloacal apertures and according to their state of contraction. *Aplidium macrolobatum* has similar large lobes around the apertures, but it has sand embedded in the test, and only 5 stomach folds.

Aplidium ornatum n.sp.
(Fig. 92)

? *Aplidium multiplicatum*: Kott, 1963, p.103 (part, specimens from Currumbin).

Distribution

Type Locality: Queensland (Wistari Reef, NW corner, low tide under rubble near reef edge, coll. P. Kott 3.11.86 holotype QM GH5157).

Further Record: ? Queensland (Currumbin — AM Y3994 Kott 1963).

Description

External Appearance: The colony is small (5mm high), mushroom-shaped, with a flat top about 1cm in diameter. The diameter reduces toward the base. Sand is present around the outside of the colony but is absent from the upper surface and internally. Zooids are arranged in circular to elongate systems opening on the upper surface. The 3 or 4 common cloacal apertures are large and protruding, sometimes in the centre of a circle of zooids, but sometimes at one end of a

double row of zooids. In life the zooids are 'ruby' and the test 'isabella' coloured (Ridgeway 1886).

INTERNAL STRUCTURE: The zooids are vertical, with the long posterior abdomina extending into the base of the colony. Thorax and abdomen are together about 3mm long. The atrial tongue from the upper rim of the opening is undivided or divided into 3 pointed lobes. There are 12 rows of stigmata, and the maximum number per row is about 10, although the holotype is contracted and the exact number difficult to determine. The stomach wall is folded longitudinally into 25 folds.

Two large embryos are in the atrial cavity of the holotype. The larval trunk is 0.66mm long. In each interspace between the middle and the dorsal and ventral adhesive organs respectively, is a median ampulla with a bi-lobed lateral ampulla on each side. Dorsal and ventral clusters of numerous epidermal vesicles extend posteriorly from the anterior end of the larval trunk. The tail is relatively short, extending about two-thirds of the way around the trunk.

REMARKS

The distinctive characters of this species are its relatively narrow thorax, numerous stomach folds, and larvae with epidermal ampullae and numerous vesicles. *Aplidium incubatum* has a similar colony to the present species, but its circular systems are more regular and its larvae have median and lateral vesicles rather than the ampullae of the present species.

Aplidium multiplicatum, which it otherwise resembles in the colour of the zooids, and the bran-

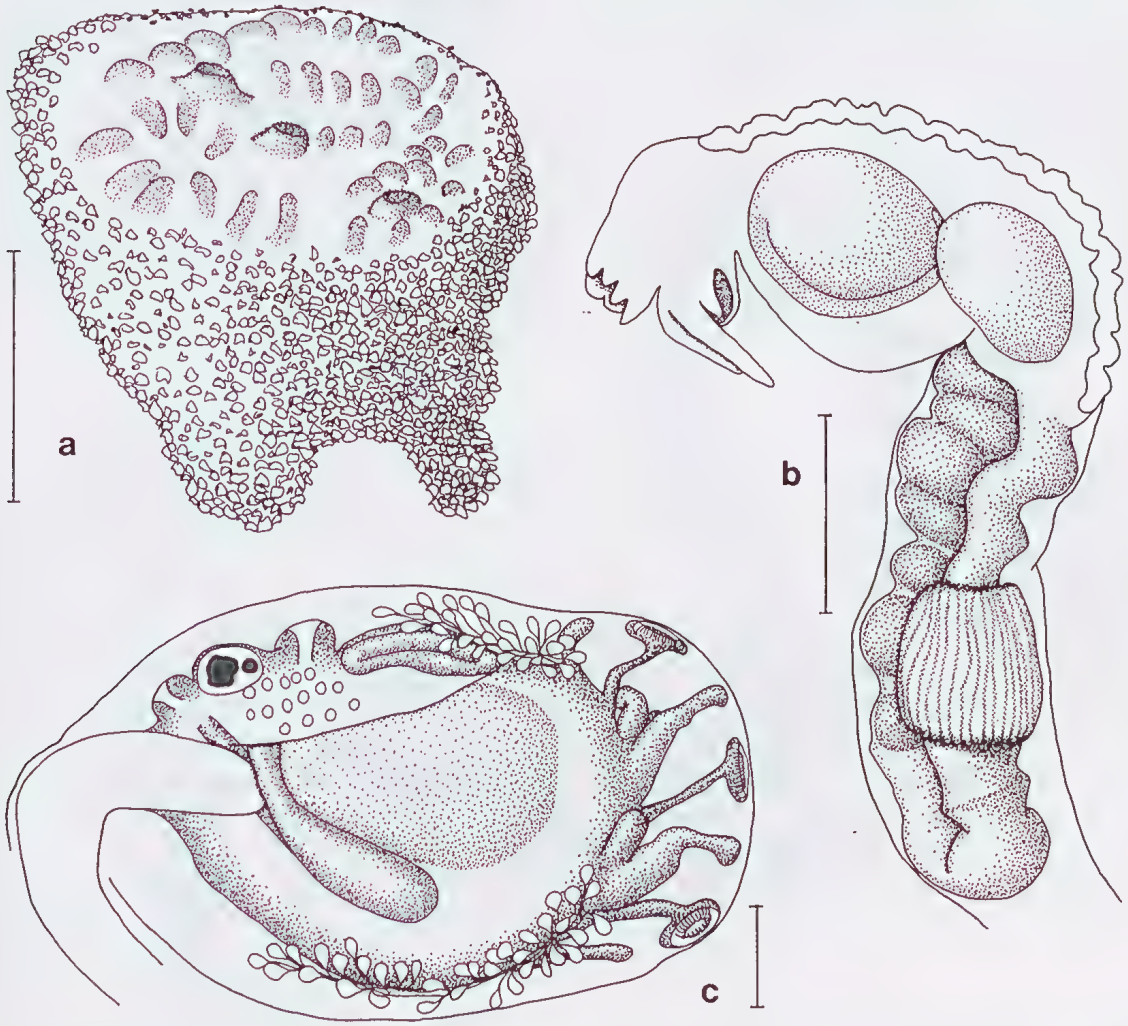


FIG. 92. *Aplidium ornatum* n.sp. (holotype QM GH5157) — **a**, colony; **b**, thorax and abdomen; **c**, larval trunk. Scales: **a**, 5mm; **b**, 0.5mm; **c**, 0.1mm.

chial sac and stomach folds, is distinguished by having single arcs of epidermal vesicles in the larval trunk, sand absent from around the border of the colony, a softer test, opaque white pigment particles around the branchial apertures and long branching double-row systems. The specimen from Currumbin assigned to *A. multiplicatum* by Kott (1963) has sand around the base and sides of the colony, but not in the upper suface or embedded. The zooids are small, contracted, and appear to be arranged in circular systems. The atrial lip is from the upper rim of the aperture, and there are 18 stomach folds. Other details of their morphology are obscured.

Aplidium uteute has numerous stomach folds, but is distinguished by its smaller circular systems, completely naked colonies, more numerous stigmata per row but fewer rows, single arcs of larval epidermal vesicles, and, usually, the absence of red pigment from the thorax. *Aplidium altarium* (Sluiter, 1909) has numerous stomach folds and colonies of similar dimensions to the present one, but the 9 or 10 rows of stigmata have about 25 per row, the posterior abdomen is short with bunched male follicles, and unlike the present species, the colony is transparent.

Aplidium paralineatum n.sp.
(Fig. 93)

DISTRIBUTION

TYPE LOCALITY: Tasmania (45 nautical mls NNE of Sister I., 39°00'S 148°25'E, 92m, sand bottom, epibenthic sled, CSIRO Statn 22, coll. W. Zeidler 14.10.84, holotype SAM E10648).

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: The specimen is a long (3cm), narrow cushion, broken at one end. It probably is a piece from a longer colony. A conical prominence about 1cm high with a terminal common aperture is at the other end. Zooids are in parallel double rows, a row along each side of the long, straight cloacal canals that run the length of the colony, converging to the large, sessile cloacal aperture. Long ridges separate the double rows of zooids from one another. The test is relatively soft, although sand is embedded throughout. Along the under surface the test is produced into fine root-like processes, which, with their adherent sand, create a felt-like mass holding the colony in the sandy substrate. The colony appears to have been organised in a single

FIG. 93. *Aplidium paralineatum* n.sp. (holotype SAM E10648) — **a**, colony; **b**, thorax and abdomen. Scales: **a**, 5mm; **b**, 0.5mm.

cloacal system, although there may have been a second cloacal aperture at the mutilated end.

INTERNAL STRUCTURE: The zooids are robust. However, the thorax and abdomen together are only about 3mm. The posterior abdomen is long and threadlike. The atrial tongue is relatively small, pointed, and produced from the anterior rim of the aperture. There are 15 rows of stigmata although these zooids are too contracted to determine the number in each row. The stomach is small with 5 deep folds in its wall. A single series of testis follicles are in the posterior end of the long posterior abdomen.

REMARKS

The species is distinguished by its long double row systems and sessile colonies. Similar long systems are in the stalked colonies of *A. australiense* which, however, has more numerous stomach folds than the present species.

Aplidium parastigmaticum n.sp.
(Fig. 94)

DISTRIBUTION

TYPE LOCALITY: Queensland (Heron I., reef slope 10m, coll. S. Cook 28.4.88, holotype QM GH5603).
FURTHER RECORD: Queensland (Heron I., QM GH5604)

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are sessile spheres about 3cm in diameter. The test is firm and translucent, with some sand on the ridges between the systems. Living zooids are vermilion with buff coloured branchial apertures. In preservative both zooids and test are pinkish.

Zooids are arranged in circular to star-shaped systems, about 7mm in diameter. The cloacal cavity is large, with some peripheral extensions to reach the zooids in the outer periphery of each of the systems. The test is soft, and the zooids all lie parallel to one another. Sand is embedded in the basal test, but not elsewhere.

INTERNAL STRUCTURE: Zooids are large and robust, about 7mm in overall length even when contracted. In the contracted zooid the posterior abdomen is about half and the thorax is slightly more than one quarter of the total zooid length.

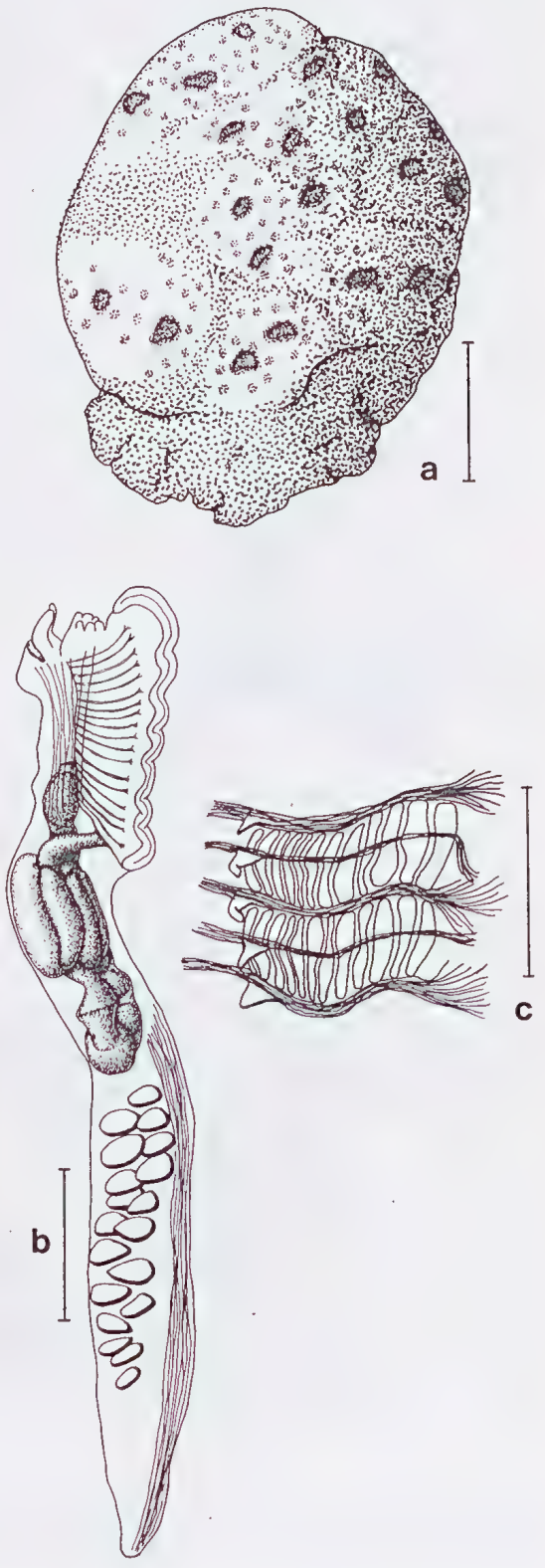


FIG. 94. *Aplidium parastigmaticum* n.sp. (holotype QM GH5603) — **a**, colony; **b**, zooid; **c**, portion of branchial sac showing muscle fibres in primary transverse and parastigmatic vessels. Scales: **a**, 1cm; **b**, 1mm; **c**, 0.5mm.

The longitudinal muscles tend to form a band in the dorsal half of each side of the thorax, and then continue in a wide band along the ventral part of the abdomen and posterior abdomen. Their contraction causes the thorax to curve around the shortened dorsum. Strong transverse muscle fibres are in the primary transverse and parastigmatic branchial vessels. They separate into short terminal branches on each side of the endostyle. The branchial aperture is 6-lobed, and the atrial aperture has a fleshy lip from the upper border of the opening. The tip of the atrial tongue is either undivided, or divided into 2 or 3 lobes. The forward pointing atrial aperture opens from a pouch

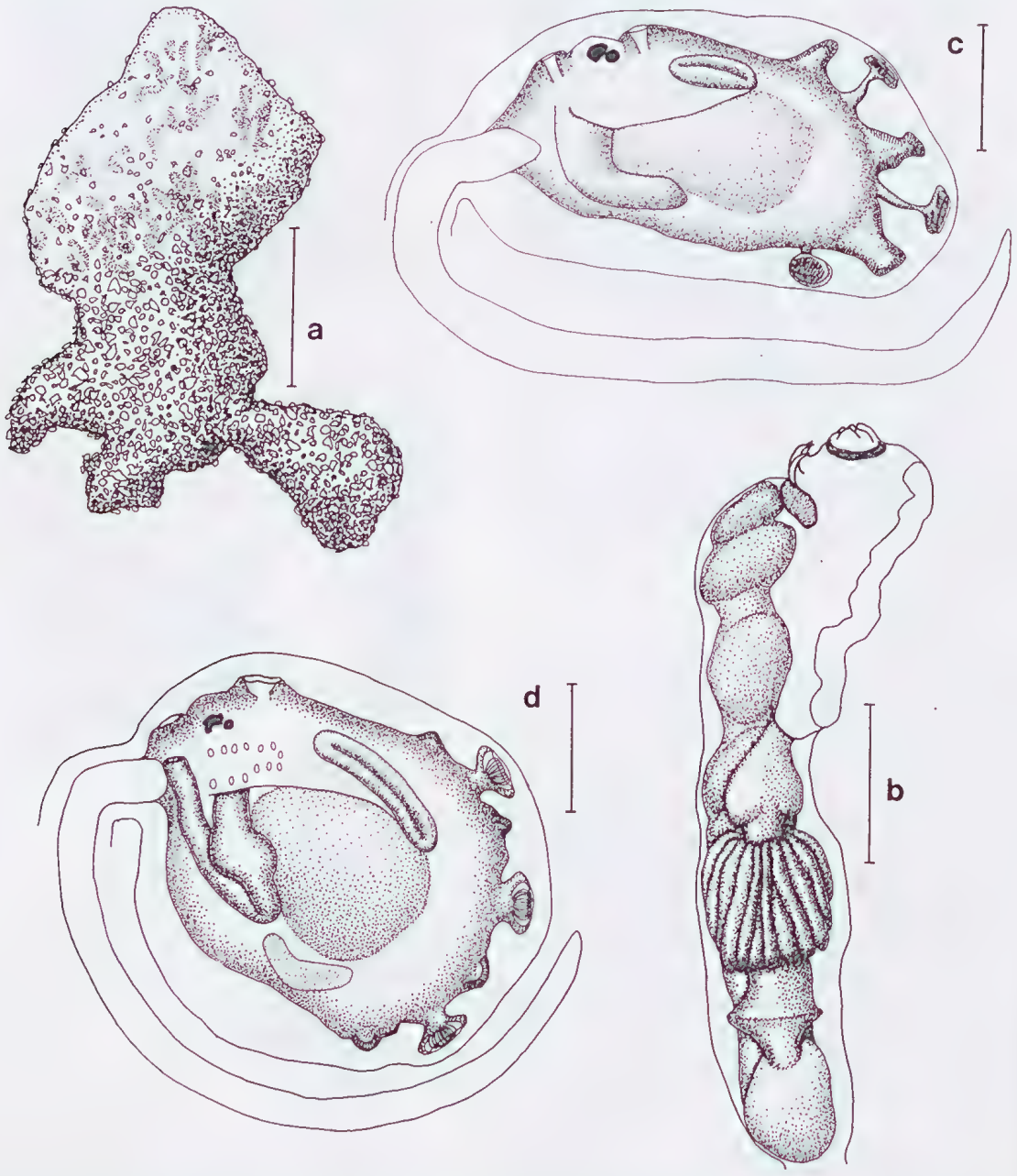


FIG. 95. *Aplidium parvum* — **a**, colony (AM Y1425); **b**, thorax and abdomen (AM Y1425); **c**, mature larva (AM Y1418); **d**, immature larva (AM Y1418). Scales: **a**, 5mm; **b**, 0.5mm; **c**, **d**, 0.2mm.

in the atrial cavity, which does not contract with the contraction of the dorsal part of the zooid. The stigmata are in 18 rows, with about 12 per row. Each row is crossed by a conspicuous parastigmatic vessel. A dorsal languet is on each parastigmatic, as well as on each primary transverse vessel.

The stomach at mid-abdominal level, has 5 distinct longitudinal folds. The male follicles are in two longitudinal series.

REMARKS

The red zooids in the translucent test resemble *A. uteute* which, however, has close circular systems (rather than the star-shaped ones of the present species) and more numerous stomach folds. The parastigmatic vessels, the atrial lip from the upper border of the opening, the pouch that forms beneath the atrial aperture when the zooid is contracted. The large stomach with 5 folds, and the parastigmatic vessels all occur in the temperate *Aplidium amorphatum* which is distinguished by its 8 branchial lobes, distinct circular systems, and poorly developed gastric folds. *Aplidium protectans*, which extends further north than *A. amorphatum* but has the same large zooid and atrial and branchial apertures, has distinct circular systems opening to depressions in the surface, and lacks parastigmatic vessels.

Some features of the present colony, such as the stellate systems, and surface sand between them, are reminiscent of *A. clivosum*. However, the atrial lip is separate from the aperture in *A. clivosum*, the zooids are larger than those of the present species and there are no parastigmatic vessels. It appears, therefore, that the colony is a member of a formerly undescribed species.

Aplidium parvum Kott, 1963
(Fig. 95)

Aplidium parvum Kott, 1963, p.112.

DISTRIBUTION

NEW RECORDS: None.

PREVIOUSLY RECORDED: Western Australia (Albany — AM Y1425 Kott 1963). Victoria (San Remo — AM Y1418 Kott 1963).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are small spherical transparent heads on short stalks to 1cm high overall. The zooids are arranged in longitudinal rows, converging to a common cloaca on the top of the head.

INTERNAL STRUCTURE: Zooids are small, the length overall extending to about 6mm. The posterior abdomen is up to twice the length of the remainder of the zooid. The short branchial siphon has 6 lobes around the aperture. The atrial aperture has a short, undivided lip from the anterior rim of the opening. Stigmata are in 12 rows of about 8. The short stomach has 18, mostly parallel, folds. The oesophagus has a pronounced prestomach enlargement at its distal end. Three embryos are incubated in a brood pouch that projects from the thorax in the syntypes (AM Y1418) collected in October.

The larval trunk is 0.8mm long. Anteriorly, single median ampullae are in the interspaces alternating with the adhesive organs. These median ampullae have columnar cells on them, and when well developed they become flat-ended rather than conical, the stalks of the adhesive organs become shallower and saucer-shaped, with long, slender stalks.

REMARKS

The small colonies, zooids and larvae are all distinctive. Although the systems resemble those of *A. altarium, A. geminatum, A. inflorescens* and *A. brevilarvacium*, the colonies are smaller, and stomach folds and stigmata are fewer. Like the present species the larva of *A. inflorescens* lacks epidermal vesicles. However, its trunk is about twice the length of that of the present species, and is further distinguished by the presence of lateral as well as median ampullae. *Aplidium geminatum, Aplidium altarium* and *Aplidium brevilarvacium* have different larval epidermal vesicles from the present species, and larger larval trunks (about 1mm long). Further, *Aplidium altarium* has appreciably more stigmata per row than the present species, *A. brevilarvacium* has fewer stomach folds (10), and in *A. geminatum* the stomach folds are more numerous.

Aplidium petrosum n.sp.
(Fig. 96. Plate 15d–f)

DISTRIBUTION

TYPE LOCALITY: South Australia (Cape Jaffa, Margaret Brock Lighthouse, coll. AIMS Bioactivity Group 18.2.89, holotype QM GH5454).

FURTHER RECORDS: South Australia (The Gap, QM GH4165–6; Hopkins I., QM GH4190).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are rigid, sandy, flat lamellae, about 1cm thick, which di-

vide and curve to form a large 3-dimensional maze. Zooids open on both sides of the lamellae. They are arranged along each side of cloacal canals that surround circular to elongate zooid-free areas. Common cloacal apertures are at the junctions of the cloacal canals. The test is slightly depressed over the cloacal canals in the preserved specimens. Sand is densely packed in the test and obscures the systems. Zooids, lying parallel to one another, are tightly enclosed in the test.

INTERNAL STRUCTURE: Zooids are small and slender, the thorax and abdomen together being about 2mm long. The branchial siphon is short and the aperture small with 6 short, rounded lobes. The small atrial lip is pointed or bipartite and projects from the anterior rim of the opening. Stigmata are in 9 rows with only 6 per row, in the narrow thorax. The stomach is long and narrow with 5 longitudinal folds. The posterior abdomen is about twice the length of the rest of the zooid, with male follicles in double rows; or when the zooid is contracted, drawn up into a bunch behind the gut loop.

Three embryos are being incubated in the atrial cavity of specimens collected in April (QM GH4165). The larval trunk is about 0.8mm long. Single large, conical, median ampullae alternate with the adhesive organs; which have slender stalks that expand into a cone at the base. A wide band of epidermal vesicles is along each side of the median line around the anterior half of the trunk.

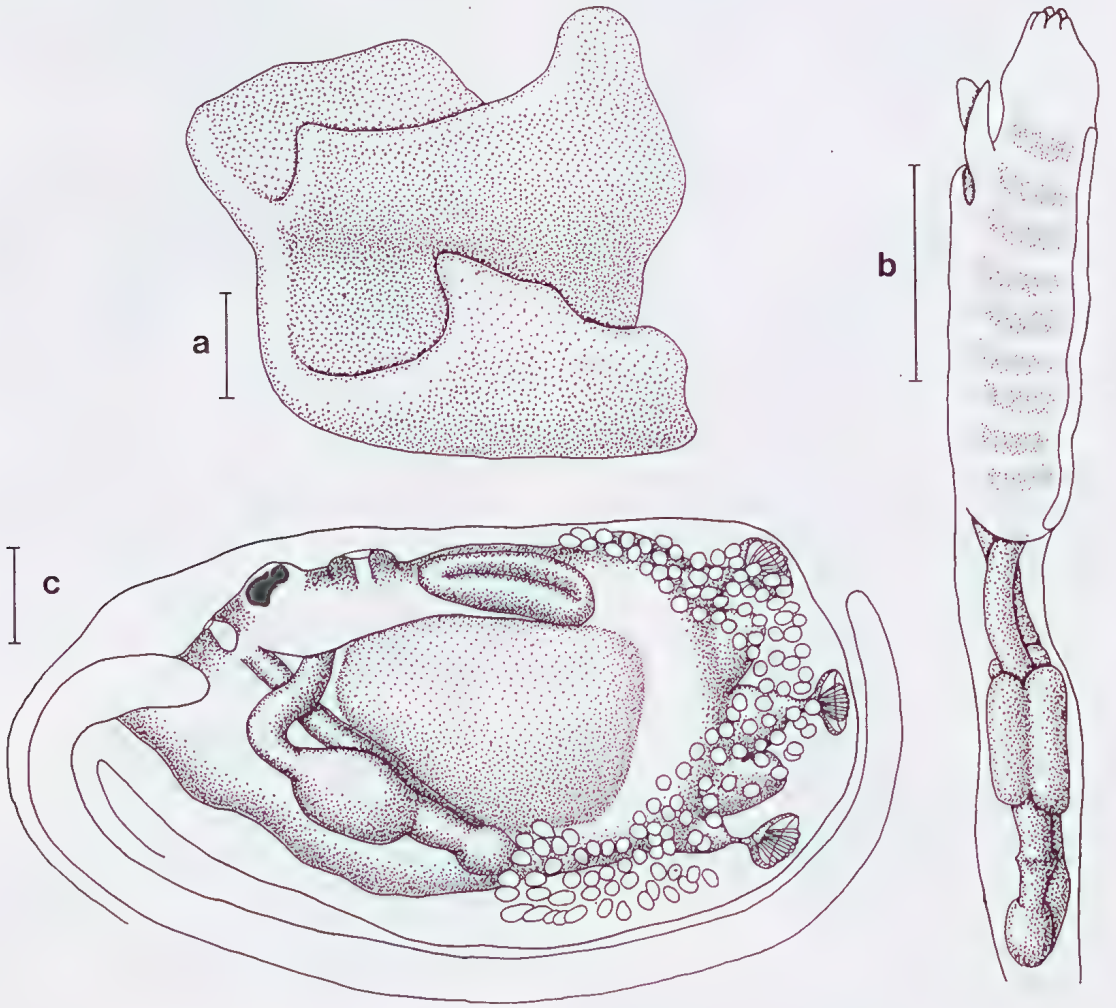


FIG. 96. *Aplidium petrosum* n.sp. — **a**, part of colony (QM GH5454); **b**, thorax and abdomen (QM GH5454); **c**, larval trunk (QM GH4166). Scales: **a**, 1cm; **b**, 0.5mm; **c**, 0.1mm.

REMARKS

Colonies forming stiff sandy lamellae are known also for *A. solidum* from the eastern and north-western coasts. They also have similar zooids, arranged in similar systems. The present species is distinguished by its more branched colony (*A. solidum* having upright lamellae rather than a 3-dimensional maze); and by the larvae which are larger than those of *A. solidum* (0.5 to 0.6mm long trunk) and have median ampullae (not present in *A. solidum*).

Aplidium ritteri have similar zooids with the atrial lip from the upper rim of the opening, but also have smaller larvae than those of the present species and long straight cloacal canals.

Aplidium protectans (Herdman, 1899)
(Fig. 97. Plate 16a,b)

Amaroucum protectans Herdman, 1899, p.73.
Aplidium protectans: Kott, 1963, p.102.
Aplidium longithorax Monniot, 1987, p. 525.

DISTRIBUTION

NEW RECORDS: Queensland (Capricorn Group, QM GH5562 GH5574; central Great Barrier Reef, QM GH5362 GH5378; Lizard I., QM GH332 GH5553 GH5611–2; far nothern Great Barrier Reef, QM GH5336).

PREVIOUSLY RECORDED: New South Wales (Montague South — Kott 1963; Port Jackson — Herdman 1899). New Caledonia (Monniot 1987).

The species is recorded from 0 to 100m depth.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are firm, gelatinous naked domes, spheres or cushions 2.5cm to 6cm in maximum dimension. The test is translucent both living and in preservative, and the zooids are pink, yellowish or orange. Circular systems, each of from 10 to 16 zooids are evenly distributed around the outer surface of the colony, and are slightly depressed into the surface in preserved colonies. The common cloacal apertures are in the central of each system. Systems are well spaced and never crowded. They appear as regular daisy-like patterns over the surface of the colony.

INTERNAL STRUCTURE: Zooids are large and robust, the thorax and abdomen even in contracted specimens together being more than 4mm long, and the posterior abdomen about the same length. The branchial siphon has 8 rounded lobes, the atrial siphon is produced out toward the central common cloacal aperture and an undivided, fleshy atrial lip arises from just above the sphincter muscle in the rim of the opening. In some zooids the atrial lip appears to be part of the rim of the siphon, but in others the atrial siphon is close to, but separate from its lip. The blunt tip of the atrial lip is divided into 3 to 6 characteristically regular, short, finger-like rounded lobes. The body wall is muscular with about 20 longitudinal bands on each side of the thorax, extending along the length of the zooid in a wide lateral band on each side. Stigmata are in 18 to 24 rows with about 20 per row. The oesophagus is relatively long, opening into a long barrel-shaped stomach with 5 shallow folds about one third of the way down the abdomen. When contracted the stomach wall tends to be drawn into horizontal folds. There is a short thick duodenum, but the remainder of the post-pyloric part of the descending limb of the gut loop is long, curving around in a corkscrew spiral, which may be a homologue of the posterior stomach, although it is longer than usual. A narrow, short section of mid-intestine intervenes between this thick distal end of the descending limb and the rectum. The rectal caeca are not well developed.

Two or 3 large eggs are present just behind the gut loop, separated from the pear-shaped male follicles which are in one or 2 longitudinal series in the remainder of the posterior abdomen or, if the longitudinal body muscles are sufficiently contracted, bunched. Up to 3 embryos, brown in preservative, are lined up in the posterior part of the atrial cavity of specimens collected in August (QM GH5362) and tailed larvae are present in colonies from Lizard I. collected in June (QM GH5553). The larval trunk is 0.8–0.9mm long. It has single median ampullae between and dorsal and ventral to the adhesive organs, and 4 clusters of epidermal vesicles, one on each side of the dorsal and ventral mid-lines behind the adhesive organs.

REMARKS

The large zooids in conspicuous circular systems, larvae with median ampullae and ventral and dorsal clusters of vesicles, and fleshy colonies are characteristic. Kott (1963) also noted the tendency for the stomach to collapse in horizontal folds in contracted zooids from a specimen from NSW waters - which was found on a crab.

Polycitor giganteum (also found on crabs) has similar large, firm, gelatinous colonies which may be a convenient consistency for the crab to hold in place and trim to an appropriate regular size and shape.

Colonies and zooids resemble *Aplidium amorphatum* in having 8 rather than 6 branchial lobes. The present species has firmer colonies a longer thorax and abdomen, and it lacks parastigmatic vessels. Larvae, although smaller, have median ampullae and dorsal and ventral vesicles like *A. lunacratum*.

Aplidium indicum (Renganathan and Monniot, 1984) from India has a similar fleshy colony to the present species and equally shallow stomach folds. However, the small, extended zooids of the Indian species were not seen to be arranged in circular systems, and have fewer rows of fewer stigmata than the present species.

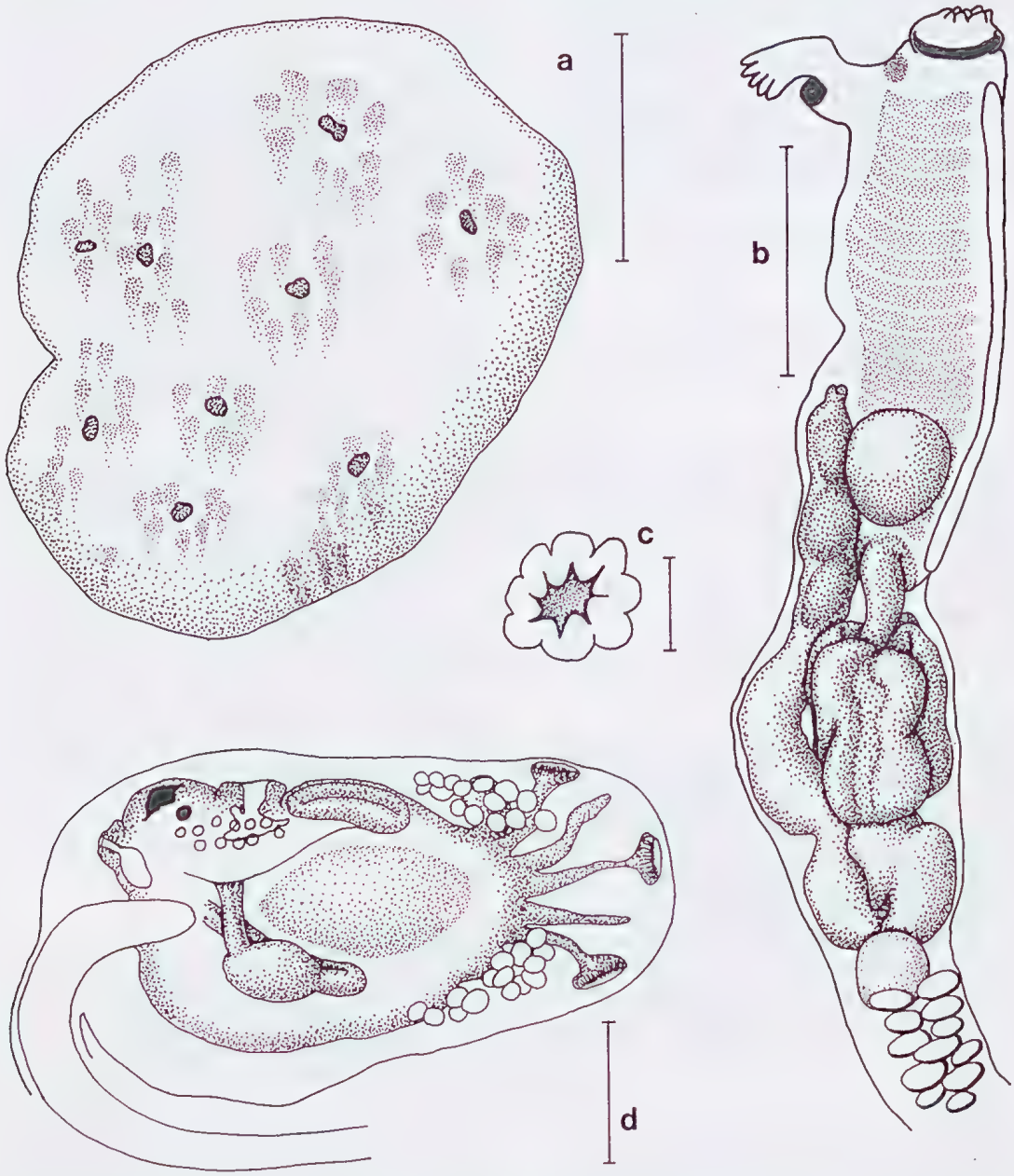


FIG. 97. *Aplidium protectans* — **a**, small colony (QM GH5329); **b**, thorax, abdomen and anterior part of posterior abdomen showing digitiform tip of atrial lip and large stomach (QM GH5553); **c**, branchial aperture from above

Aplidium ritteri (Sluiter, 1895)
(Fig. 98)

Amaroucium ritteri Sluiter, 1895, p. 10.
Aplidium lobatum: Tokioka, 1967, p.22. ? Nishikawa, 1984a, p.110. Monniot, 1987, p.525. Monniot and Monniot, 1987, p.73.

DISTRIBUTION
NEW RECORDS: Queensland (Capricorn Group, QM GH5649 GH5660 GH5685 GH5704 GH5779–81).
PREVIOUSLY RECORDED: Queensland (Torres Strait — Sluiter 1895). Western Pacific (Palau Is, New Caledonia — Tokioka, 1967, Monniot, 1987; Truk, Ponape — Nishikawa 1984a). French Polynesia — Monniot and Monniot 1987).

The species is a tropical one.

DESCRIPTION
EXTERNAL APPEARANCE: The colonies are investing sheets or lumpy and massive with a relatively even surface and sand embedded throughout. The ridges that separate the long double rows of zooids are relatively inconspicuous, and the zooid openings along each side of the cloacal canals between these long ridges often are obscured by the embedded sand. Common cloacal apertures are at the junctions of 2 or more canals. Living colonies, are described as 'sandy with pink', and 'solid, sandy'.

INTERNAL STRUCTURE: Relaxed zooids are about 3mm long. The thorax is about half the total length and the abdomen and posterior abdomen each half of the remainder. The 6 branchial lobes are well-formed and triangular. The atrial aperture is small and rounded with a short, pointed atrial lip from the anterior rim of the opening. A conspicuous bulging sphincter is behind the branchial lobes. The body muscles are strong and the short posterior abdomen is often drawn up into a short clump behind the abdomen.

Stigmata are in 11 or 12 rows of up to 8 in the narrow pharynx. The most ventral and dorsal in each row are short. The oesophagus is moderately long, and the stomach is divided into 5 by the deep folds in its wall. There is a long, narrow duodenum, narrow proximal part of the mid-intestine and an oval posterior stomach in the end of the descending limb of the gut loop.

The posterior end of the posterior abdomen is curiously flattened and straight edged. Up to 8 male follicles alternate with one another, or they are in a single series in the relaxed posterior abdomen; when the zooid is contracted they are bunched together. Male and female gonads are not present together in the one zooid. Embryos are incubated in the atrial cavity of specimens collected in November (QM GH5649) the tailed larva is small, the trunk 0.47 to 0.57mm long, with the tail wound three-quarters of the way around it. The adhesive organs are relatively deep

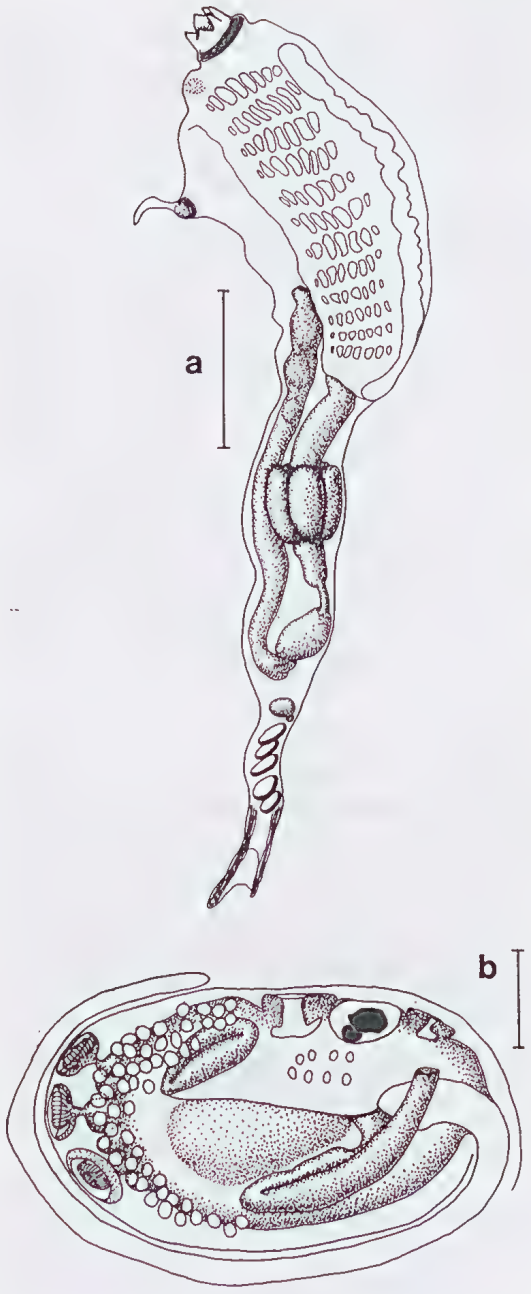


FIG. 98. *Aplidium ritteri* — **a**, zooid (QM GH5779); **b**, larva (QM GH5649). Scales: **a**, 0.5mm; **b**, 0.1mm.

axial cones in epidermal cups. The base of their stalks expand into wide cones. Short median ampullae alternate with them. The anterior end of the larval trunk is obscured by a long, wide lateral arcs of epidermal vesicles.

REMARKS

The specimens described above have all the characters of the type from Torres Strait, with the atrial lip from the upper rim of the opening, about 12 to 14 rows of 6 or 7 stigmata, 5 stomach folds, and furrows and ridges on the upper surface of the colony. The species has much in common with the Red Sea *Aplidium lobatum* Savigny, 1816 with which it often has been confused. The principal differences between these species are the larger branchial sac of *A. lobatum*, with up to 12 stigmata per row, and the division of the upper surface of the colony into more or less regular flat-topped, oval cushions, separated from one another by narrow furrows (see Michaelsen 1920). *Aplidium macrolobatum* n.sp. has a longer atrial lip, more stigmata per row, and median vesicles in the larva as well as lateral ones.

In Australian waters the temperate and east-coast species *Aplidium solidum* has much in common with the present one, having sandy colonies, the atrial lip from the upper rim of the aperture, 12 rows of up to 7 stigmata, 5 stomach folds and bunched male follicles in a short posterior abdomen with a flattened straight-edged tip. *A. ritteri* has straight rows of zooids in contrast with the curved ones surrounding circular zooid-free elevation of the test in *A. solidum*. Although this appears to be a minor difference, the larvae constitute more compelling evidence that the species are separate — the larvae of *A. solidum* lack median ampullae but their trunk length (0.4 to 0.5mm) overlaps the range in the present species.

Aplidium caelestis has similar sandy colonies, but more distinct long, double-row systems and zooids with the atrial tongue separate from the aperture.

Aplidium robustum n.sp.
(Fig. 99. Plate 16c)

Aplidium flavolineatum: Kott, 1975, p.5.

DISTRIBUTION

TYPE LOCALITY: Western Australia (King George Sound, Albany, small breaking reef, south of Mt Martin, 35°0.8'S 117°57.0'E, 2.0m, in small crevices in flat base rock, coll. AIMS Bioactivity Group 27.3.89, holotype QM GH5467; paratype QM GH5506).

FURTHER RECORDS: South Australia (Great Australian Bight — SAM E2595 Kott 1975). Tasmania (Dunnalley, TM D1866).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are sessile, spherical or conical to 8cm high and 6cm in greatest (basal) diameter. The test is soft and gelatinous, but turgid and opaque, cloudy beige in preservative. In life the colony is pink around the common cloacal apertures and white over the zooids. Zooids are in circular, oval or elongate systems around and converging to the common cloacal apertures, which are numerous, large, sessile, and scattered randomly over the surface. They are said to 'turn to slits' when the colony is touched. Sand is present on the basal surface of the South Australian specimen, which is smaller than the others.

The zooids are perpendicular to the surface but posteriorly criss-cross one another in the centre of the colony. A sheath of soft test containing opaque white corpuscles clings to the zooids.

INTERNAL STRUCTURE: Zooids are robust, the contracted thorax and abdomen together being about 3mm and about equal in length. When relaxed the thorax probably is longer than the abdomen. About 15 longitudinal muscles are on the thorax and extend the length of the zooid. The 6 branchial lobes are small and round. The atrial lip from the upper rim of the aperture has a fleshy lip divided into 2 or 3 pointed lobes, or undivided with or without smaller lobes on each side. Stigmata are in 14 to 16 rows of up to 12. The oesophagus is moderately long, and the relatively small stomach, in the middle third of the abdomen, has 20 longitudinal, parallel folds in its wall. The duodenum, mid-intestine and posterior stomach are in the posterior third of the descending limb of the gut loop. There are rectal caeca at the proximal end of the rectum.

Up to 3 embryos are in the atrial cavity of the type material, of which one may be a well-developed tailed larva. The larval trunk is long (1mm), and almost cigar-shaped. The tail reaches to its anterior end. A lateral ampulla is on each side of the conical or cylindrical median ampullae that is in each interspace between the adhesive organs. The median ampulla between the middle and ventral adhesive organs is divided into 2. A cluster of epidermal vesicles is along each side of the mid-dorsal and mid-ventral lines, but not around the anterior end of the trunk.

Up to 6 embryos are lined up in the atrial cavity of the South Australian specimen. The tailed lar-

vae are smaller (trunk 0.8mm long) and the lower median ampulla is not subdivided but otherwise they are similar to the larvae of the type specimens.

REMARKS

The species resembles *A. opacum* in having a sheath of soft test containing opaque white corpuscles clinging to the zooids, large fleshy colonies, and the same number of stomach folds. However zooids of the present species are more robust than those of *A. opacum*, with more rows of stigmata. They also have a larger larva with lateral ampullae and fewer vesicles than *A. opacum*.

The present species has larger opaque white cells around the zooids and firmer test than *A. multiplicatum*, and it lacks the characteristic single arc of lateral vesicles in the larval trunk.

In the distribution of epidermal vesicles this species resembles *A. ornatum* from tropical waters, although the latter species is smaller than the present one and is a different shape.

The smaller colony (*A. flavolineatum*: Kott, 1975) from South Australian waters with a layer of sand on its under surface and smaller larvae than the type may be found not to belong to the present species. However, at this stage it is possible that its differences represent no more than intraspecific variation. It was assigned to *A. flavolineatum* by Kott (1975) on the basis of its large number of stomach folds. However, the South African species has more numerous larval lateral ampullae and a brood pouch.

Aplidium gastrolineatum has many characters in common with the present species, but its common cloacal apertures are protuberant rather than sessile, and its larvae are different.

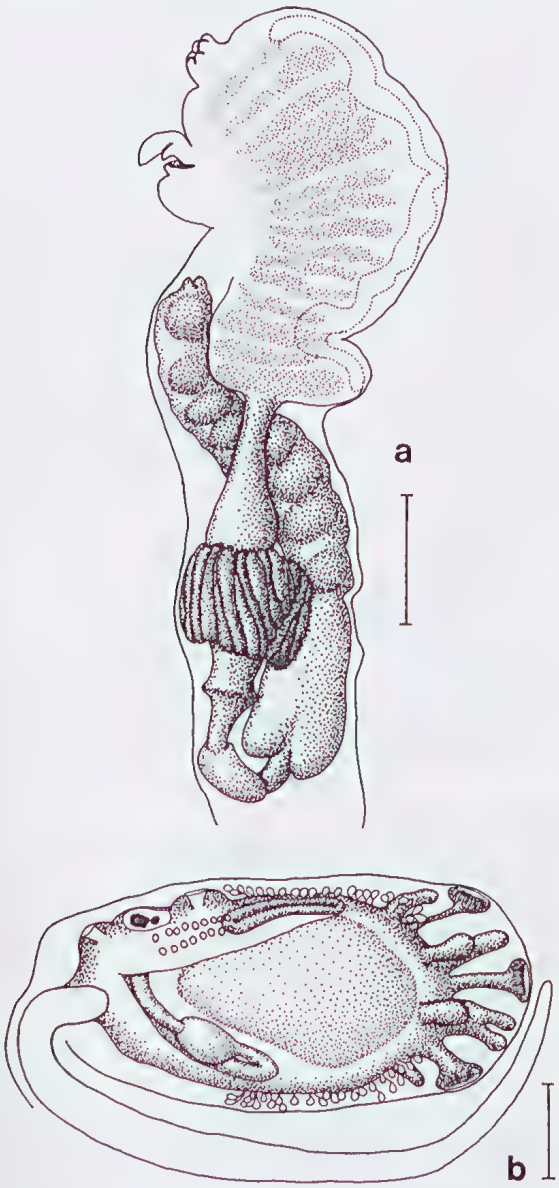


FIG. 99. *Aplidium robustum* n.sp. (holotype QM GH5467) — **a**, thorax and abdomen; **b**, larva. Scales: **a**, 0.5mm; **b**, 0.2mm.

Aplidium rosarium n.sp.
(Fig.100)

DISTRIBUTION

TYPE LOCALITY: Queensland (Heron I., Blue Pools, rubble fauna, low tide, coll. P. Kott 8.8.82, holotype QM GH 5224).

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: The firm, gelatinous colony is wedge-shaped, with a little sand embedded basally. When living the holotype was rose-purple, but in preservative it is white and cloudy, with beige-pink zooids. Zooids are along each side of long canals converging to the cloacal apertures.

INTERNAL STRUCTURE: The zooids are robust, with up to 4 embryos crowded in the atrial cavity. The longitudinal thoracic muscles are strong and the thorax and abdomen of contracted zooids are together only 2mm. The 6 branchial lobes are triangular and conspicuous. The atrial lip is fleshy and arises from the upper rim of the aperture. It has a central band of longitudinal muscles that

extend into the tip, which is pointed or divided into 3 small terminal lobes.

The stigmata are in 12 rows of about 12 per row. The short stomach wall has 20 folds. The posterior abdomen is about twice the length of the rest of the zooid.

Larvae are of moderate size, the trunk being 0.6mm long, with 2 rows of stigmata in the larval pharynx. A single arc of about 20 vesicles is along each side of the median line around the anterior end of the trunk. In immature larvae, a few median vesicles branch off the tip of the median ampulla which is in each interspace between the adhesive organs. The ampullae subsequently disappear and the stalk of each median vesicle appears to be independent, and attached directly to the larval ectoderm.

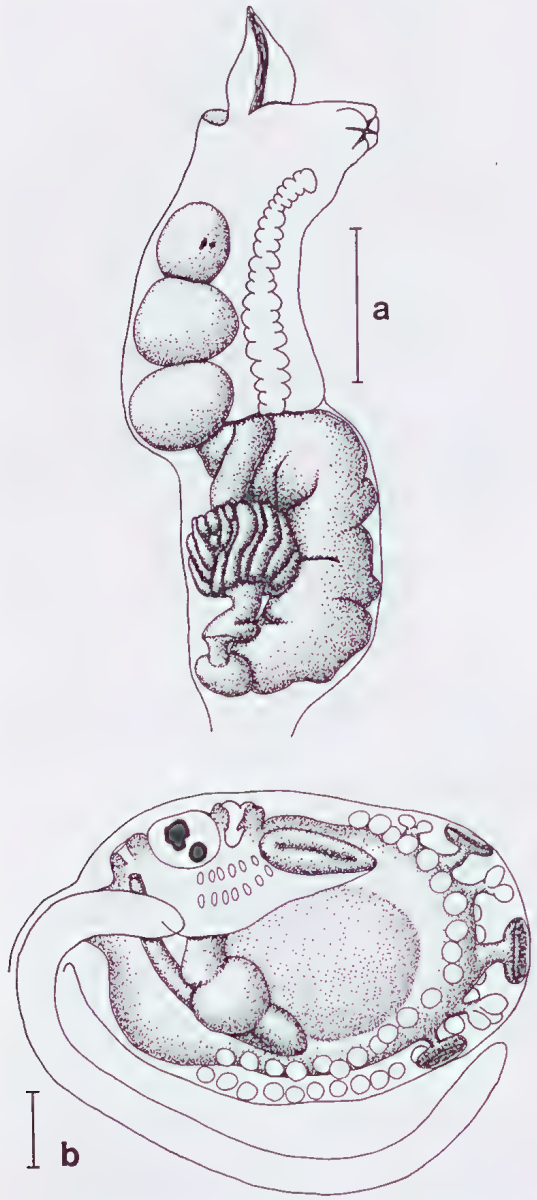


FIG. 100: *Aplidium rosarium* n.sp. (holotype QM GH5224) — **a**, zooid; **b**, larva. Scales: **a**, 0.5mm; **b**, 0.1mm.

REMARKS

Aplidium ornatum has a similar gelatinous colony, but its branchial sac is narrower and its large larvae have posterior vesicles and median and lateral ampullae, and lack the anterior arc of lateral vesicles that is present in *A. rosarium*. The larvae resemble those of *A. filiforme*, but colonies differ, and the zooids have more rows of stigmata.

The present species has some affinities with *A. altarium* but its larvae are smaller, the pharynx narrower and more muscular, and the stomach smaller with fewer folds. *Aplidium uteute* has circular systems, a brood pouch and more numerous stomach folds distinguishing it from the present species. Some aspects of the larvae suggest a relationship with *A. incubatum*, however the larval trunk of the latter species is larger, has more median vesicles and, the zooids have more stigmata and stomach folds, and are arranged in circular systems. Thus, despite the fact that only the holotype is available, the species is readily distinguished from other known species.

Aplidium rubricollum Kott, 1963
(Fig. 101. Plate 16d)

Aplidium rubricollum Kott, 1963, p. 103 (part, not specimens from Western Australia AM Y1403 < ? *A. solidum*); 1972a, p.15; 1972b, p.176.

DISTRIBUTION

NEW RECORDS: South Australia (Avoid Bay, QM GH4191; Port Noarlunga, QM G9304).

PREVIOUSLY RECORDED: South Australia (Reevesby I. — AM Y1417 holotype Kott 1963; Upper St. Vincent Gulf — SAM E2579 Kott 1972a; Pearson I. — Kott 1972b). Balnarring Beach — AM Y1415 Kott 1963).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies range from small cushions investing weed or rubble to regular oval cushions to 5cm in maximum extent but never more than 1cm thick. Sand is embedded in the internal test, becoming sparse in the upper layer around the thoraces. Sometimes it is completely absent from the upper surface of the colony, but in other colonies only the test above the

systems, including the protruding common cloacal apertures, is naked. Zooids are crowded along each side of relatively short canals that converge to the protruding cloacal apertures which are scattered over the surface, about 5mm apart. Red pigment cells are said to have been present in the surface layer of test in the living and freshly preserved specimens, and the colourless zooids are conspicuous, interrupting these. In the long-preserved specimens a brownish deposit in the surface test may be the remains of these red cells.

INTERNAL APPEARANCE: Zooids are small, with 10 fine longitudinal muscles. The atrial lip has an undivided tip which becomes bidentate through the contraction of a median band of muscles. The lip arises from the body wall close to, but separate from the opening, which is on a short protruding siphon, often flattened antero-posteri-

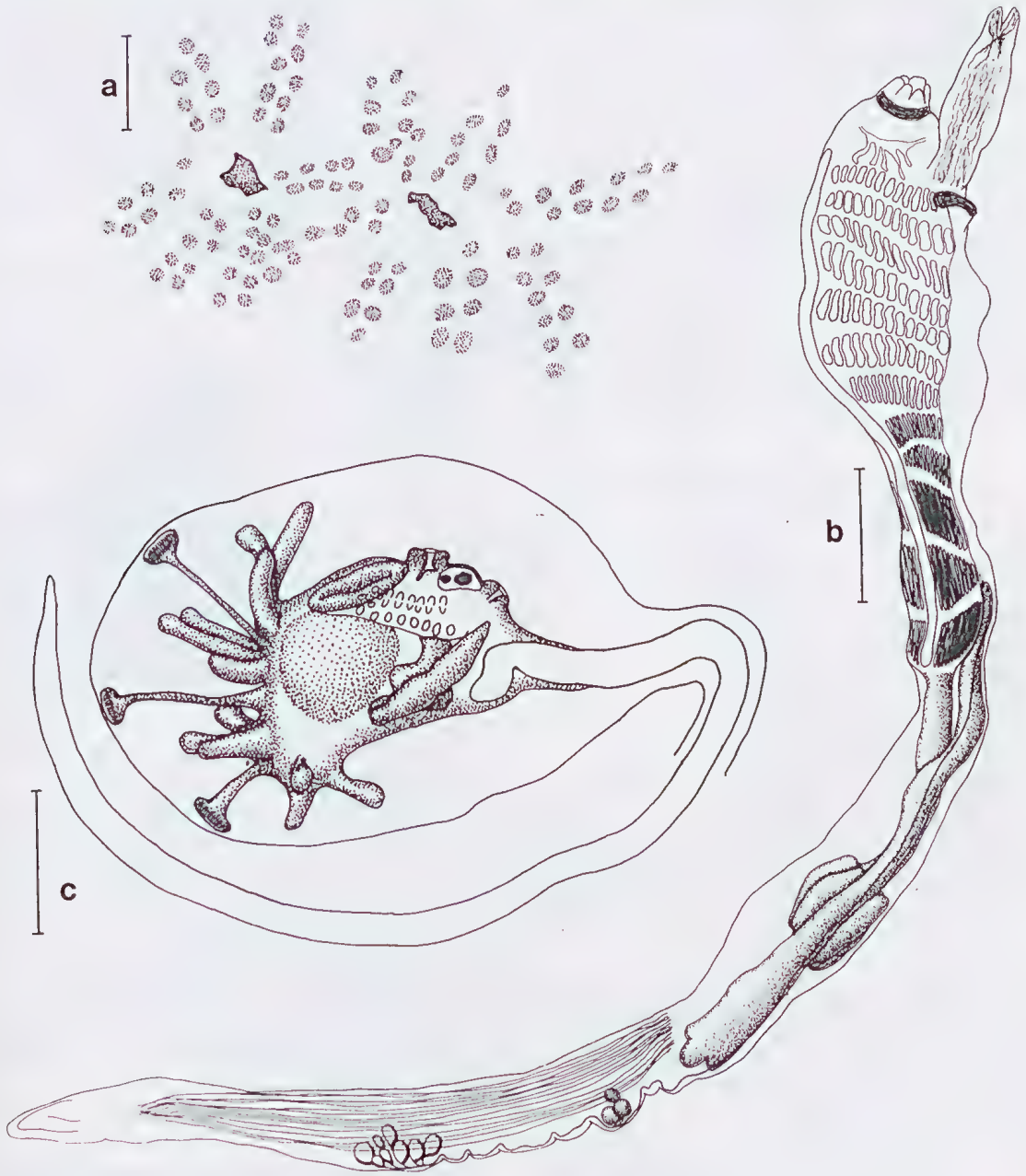


FIG. 101: *Aplidium rubricollum* — **a**, surface of colony showing 2 systems (QM GH4191); **b**, zooid (holotype AM Y1417); **c**, larva (holotype AM Y1417). Scales: **a**, 2mm; **b**, 0.5mm; **c**, 0.2mm.

orly. Stigmata are in 11 or 12 rows of up to 14. The stomach is short with 5 deep folds.

One specimen collected in February (QM G9304) and the holotype collected in December contain single, large embryos in the atrial cavity. The larval trunk is 0.7mm long. It has median and lateral ampullae, but no epidermal vesicles.

REMARKS

The systems and the colonies resemble those of *A. clivosum* except that the canals converging to the cloacal apertures are not so numerous, the zooids and systems are smaller, and the larvae lack the vesicles that obscure the anterior end of the trunk in *A. clivosum*. The zooids are small and, like those of *A. clivosum*, have the atrial aperture separate from the opening, but the present species has relatively shorter and wider thoraces with up to 12 rows of 14 stigmata while *A. clivosum* has up to 18 rows of about 12 stigmata. Colonies assigned to *Aplidium caelestis* (see above) often superficially resemble those of the present species. However, *A. caelestis* has a narrower thorax with fewer stigmata per row, the systems have longer double rows of zooids and the larvae contain epidermal vesicles.

Aplidium solidum (Herdman, 1899) (Fig. 102)

Psammaplidium solidum Herdman, 1899, p.85.
Psammaplidium lobatum: Herdman, 1899, p.85.
Psammaplidium fragile Herdman, 1899, p.86
Psammaplidium incrustans Herdman, 1899, p.87.
Aplidium solidum Millar: 1963, p.1.
Aplidium arboratum Kott, 1963, p.96.
Synoicum investum Kott, 1963, p.90.
Aplidium lobatum: Kott, 1976, p.61.
? *Aplidium rubricollum* Kott, 1963, p.103 (part, specimen from Rottnest I. AM Y1403).
Not *Amaroucium solidum* Ritter and Forsyth, 1917, p.486; Van Name, 1945, p.49. The species name is a secondary homonym and accordingly a *nom. nov.* is required for this species.

DISTRIBUTION

NEW RECORDS: Western Australia (Dampier Archipelago, QM GH5411). New South Wales (Jervis Bay, QM GH5778; Batemans Bay, AM Y2278; Bass Point, QM GH5620; Arrawarra, QM GH5777). Queensland (Point Lookout, QM GH5782).

PREVIOUSLY RECORDED: New South Wales (Botany Bay — AM U3941 Herdman 1899; Millar 1963). Queensland (Bargara — holotype AM U3928, paratype QM G4937 *S. investum* Kott, 1963).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies form extensive rigid, sandy sheets, lobes and lamellae from about 3mm to 2cm thick. These branch and fuse with one another in a vertical plane. Along their upper border the lamellae terminate in rounded margins. The upright lobes and lamellae form when the sheet is folded, fuses back to back, and extends up in the vertical plane. Sand is embedded throughout.

Zooids appear to be fairly evenly placed and close to one another, along the sides of narrow, shallow canals. Circular or oval, raised zooid-free areas sometimes are between (or surrounded by) the double rows of zooids. Common cloacal openings are scattered over the surface of the colony at the junction of the canals. The colour of the colonies is dominated by the sand, although the zooids are pinkish in preservative.

INTERNAL STRUCTURE: The zooids are small, seldom more than 4mm even in relaxed condition. Thorax, abdomen and posterior abdomen are of about equal length. Fine longitudinal muscle bands extend the length of the zooid. A sphincter muscle is at the base of the 6 pointed branchial lobes. The small, circular atrial aperture has a small lip, undivided or divided into 2 or 3 pointed lobes, from the anterior rim of the opening.

Stigmata are in 9 to 12 rows of about 6. The long, narrow stomach has 5 folds. The posterior stomach is large, oval, at the distal end of the descending limb of the gut loop. The posterior abdomen is relatively short, with a single series of up to 7 male follicles in a single longitudinal series or sometimes bunched up behind the anterior ovary. However, even when it is not contracted, the extremity of the posterior abdomen has a truncated flat appearance. A small ovary is often present anterior to the testis follicles.

Two to 5 embryos are crowded into the atrial cavity of specimens from Botany Bay from Jervis Bay in February (QM GH5778) and from South Australia in April (QM GH4165). Larvae are small, the trunk 0.4 to 0.5mm long with the tail wound half to three- quarters of the way around it. A mass of epidermal vesicles surround the 3 median adhesive organs and obscure the anterior end of the trunk, but there are no median ampullae. The base of stalks of the adhesive organs expand into a cone.

REMARKS

Like the present species, *Aplidium acroporum* n.sp. has small zooids with the atrial lip from the rim of the opening. However it has 8 stomach

folds (rather than 5), and circular systems with zooids surrounding the cloacal cavity (rather than along each side of narrow canals).

The specimen from Rottnest I. appears to have been wrongly assigned to *A. rubricollum* by Kott (1963). Both colony and zooids resemble those of the present species except in the colour (pink with red zooids), which they have retained over a long time (40 years) in preservative. The colour of the living colony is not known. Although brown to orange living specimens of *A. solidum* are known the colour of the embedded sand dominates their

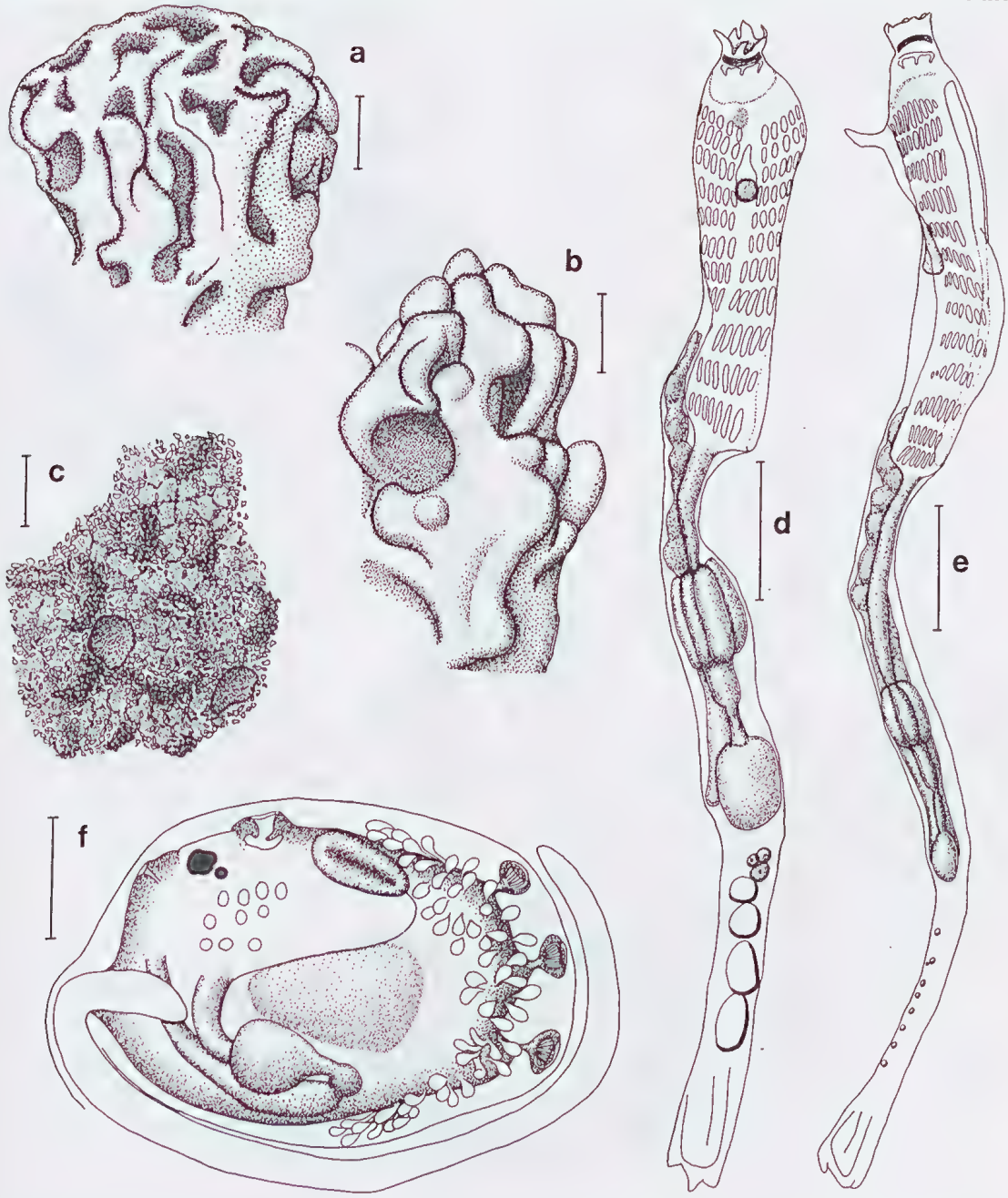
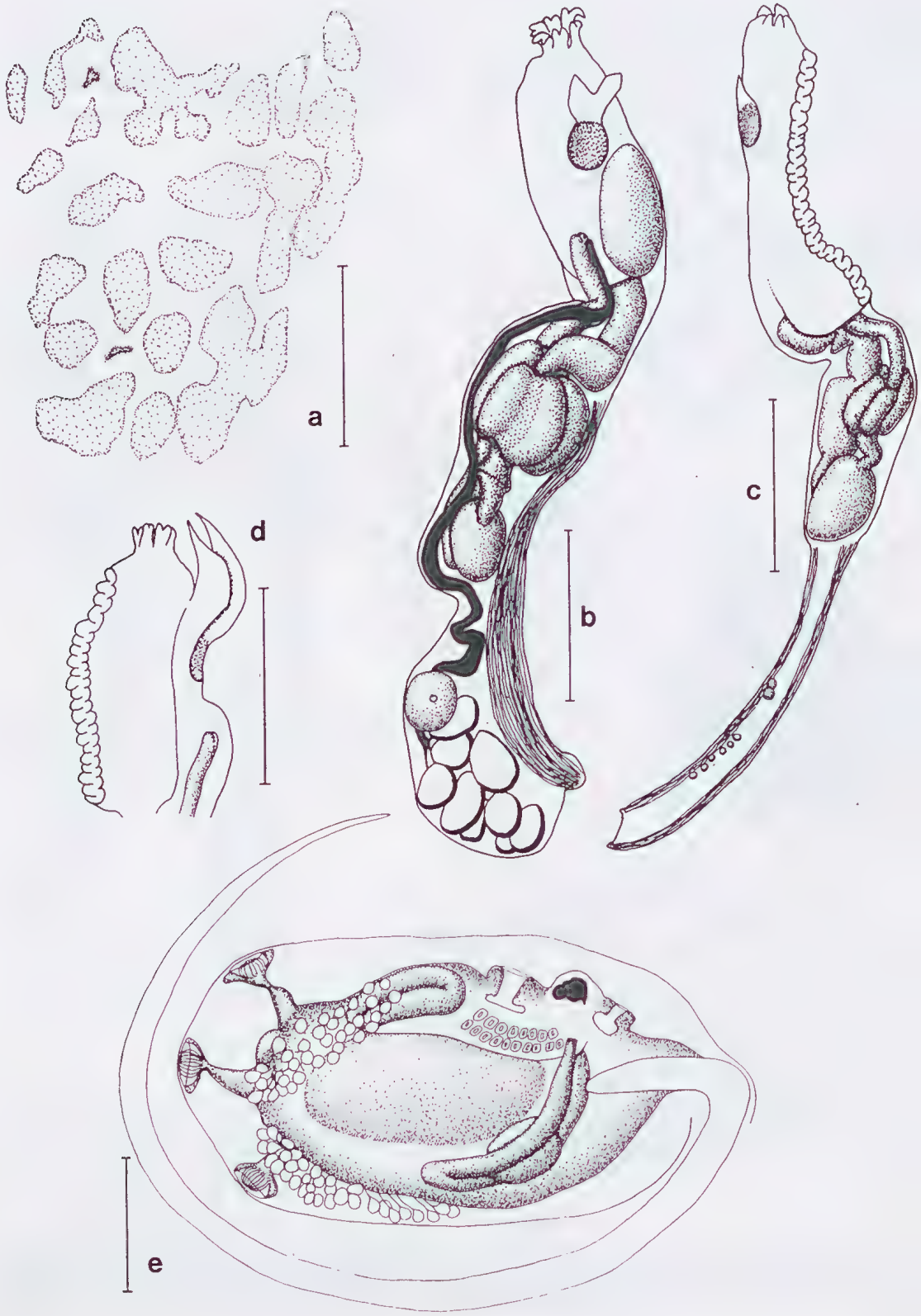


FIG. 102: *Aplidium solidum* — **a**, **b**, parts of colonies (QM G4937, AM U3941); **c**, surface of colony showing cloacal apertures at junction of the cloacal canals that surround the small zooid-free test areas (QM GH5782); **d**, **e**, zooids (QM GH5777 GH5782); **f**, larval trunk (QM G4937). Scales: **a**, **b**, 2cm; **c**, 2mm; **d**, **e**, 0.5mm; **f**, 0.1mm.


a
b
c
d
e

colour in preservative. Therefore, the specimen from Western Australia is unusual and despite similarities in its morphology it may not be conspecific with *A. solidum*.

The sandy investing colonies resemble some of *Aplidium caelestis*, although cloacal canals of the present species surround circular areas rather than the long ridges of *A. caelestis*, which also has colonies that are thicker and do not fold back to form upright lamellae as they do in the present species. Further *A. caelestis*, has zooids with longer branchial siphons, the atrial lip separate from the opening, and testis follicles in a double series in a long (rather than short, truncated) posterior abdomen.

The species resembles *Aplidium ritteri* in its sand-filled colonies, small zooids with narrow thoraces, small atrial lip from the upper rim of the opening: and short, truncated and flattened tip of the posterior abdomen. The systems of *A. ritteri* are in long and relatively straight double rows, and the larvae have a trunk 0.5 to 0.6mm long, with median ampullae as well as lateral vesicles. *Aplidium petrosum* from South Australian waters has similar systems as well as similar zooids to the present species, but is distinguished by its more complex colonies and larger larvae with median ampullae.

Aplidium tabascum n.sp.
(Fig. 103. Plate 16e,f)

DISTRIBUTION

TYPE LOCALITY: Queensland (Heron I. reef, 15m, coll. N. Coleman 5.8.77, AMPI 207, holotype QM GH5208; Heron I, reef, 9m, coll. N. Coleman 16.7.73, AMPI 85, paratype QM G9726; coll. P. Fredrickson, paratype QM GH5542; Erskine I. 5–10m, coll. Roche (SLV 12) 21.3.76, paratype QM G9727).

FURTHER RECORDS: Queensland (Capricorn Group, QM G9725 GH5513 GH5543; Swain Reefs, MV).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies form large fleshy mats or sheets to 7cm or more in maximum dimension. The surface has a 'marbled' appearance owing to irregularly shaped zooid-free areas of test, between and around which are slightly depressed areas where a relatively thin layer of surface test covers the cloacal canals. Sparse but evenly distributed sand grains are in the zooid-free solid parts of the test and sand grains are crowded into a line along the margins of these areas where zooids line the cloacal canals and the branchial apertures open to the exterior. Sand is also crowded around the margins and in the base of the colony, but is not present on the upper surface either over the common cloacal canals or the zooid-free areas they surround. Large common cloacal apertures are in the depressed areas over the common cloacal spaces and appear to be randomly distributed.

Sometimes the solid test areas are isolated from one another, forming islands surrounded by common cloacal cavities and zooids. In other specimens they are long and curved and meander through the colony between and around the cloacal spaces.

The colonies are a bright red-orange colour in life. Although a trace of the orange pigment at first persists in the preserved colony, subsequently they are white. In fresh material, the red pigment is in minute crowded spherical cells in the test and the zooids but these are not present in preserved specimens.

INTERNAL STRUCTURE: Zooids are small and narrow, 2 or 3mm long, although when contracted they are shorter with the posterior abdomen bunched and drawn up alongside the gut loop. The 6 branchial lobes around each branchial aperture have bands of muscles which sometimes are drawn in to subdivide the tip of each lobe. The atrial lip from the upper rim of the aperture is undivided or divided into 2 or 3 pointed lobes of varying size. Fine longitudinal muscle bands are on the thorax, and extend the length of the abdomen and posterior abdomen in a wide ventral band. The stigmata are in 15 rows with up to 8 per row. The stomach wall has 5 folds. The gut loop is relatively short. The posterior abdomen is club-shaped when the zooid is relaxed, with a long neck anteriorly and about 8 large male follicles in a single series in the expanded posterior part. When contracted, however, the testis follicles are bunched, and the posterior abdomen is drawn up alongside the gut loop. An ovary with 2 or 3 large oocytes is anterior to the testis follicles.

One or 2 embryos are in the atrial cavity of zooids collected in July and August (QM G9726 GH5208 GH5513) but none in March or December. The larval trunk is oval, about 0.6 to 0.8mm long, with the tail wound the whole way around it. On each side of the median line dorsal and ventral clusters of epidermal vesicles extend pos-

FIG. 103: *Aplidium tabascum* n.sp. — **a**, surface of colony showing almost continuous line of sand particles around each area of zooid-free test containing sparse embedded sand (QM GH5513); **b**, zooid (gut loop twisted to the left) (QM GH5208); **c**, sexually immature zooid (QM GH9725); **d**, thorax showing large bilobed atrial lip (QM GH5208); **e**, larva (QM GH5208). Scales: **a**, 1cm; **b–d**, 0.5mm; **e**, 0.2mm.

teriorly from opposite the base of the dorsal and ventral adhesive organs, respectively. These dorsal and ventral bands of vesicles are not continuous at the anterior end of the trunk. Neither vesicles nor ampullae are present in the median line between the adhesive organs. One larva found in the holotype had 5 adhesive organs instead of the usual 3.

REMARKS

The present species, based on a significant number of specimens, has a striking appearance with apparently stable characters showing little or no variability. It is distinguished by its double rows of zooids opening into depressions surrounding cushion-like elevations on its naked upper surface, the capacity to sort sand particles and arrange them around the margin of the zooid-free surface elevations, its red-orange colour, narrow thoraces, and the interruption of the band of lateral larval vesicles.

The same sort of cloacal systems, and the capacity to sort embedded sand particles and arrange them in the colony are properties of other *Aplidium* spp. (e.g. *A. caelestis*, *A. lenticulum* n.sp.). *Aplidium lobatum* Savigny, 1816 from Suez and *A. cellis* Monniot, 1987 from New Caledonia also have similar cloacal systems. *Aplidium caelestis* and *A. lenticulum* differ in having an atrial lip separate from the opening but the *Aplidium cellis* and *A. lobatum* have similar colonies, zooids and larvae to those of the present species, differing only in their embedded (and sometimes encrusting sand), smaller larval trunk (0.56mm long), and colour (white rather than red). Despite the description of *A. cellis*, the reported incrustation of sand on the upper surface (slightly less densely distributed over the cloacal canals) is not apparent in the published photograph (Monniot, 1987, Pl. 2B). Further, it is not clear whether the white colour recorded for the 2 New Caledonian specimens is their living colour, or their colour in preservative, or merely the colour of the sand encrusting them. Thus, in addition to the possibility that the New Caledonian species is a junior synonym of *A. lobatum*, *A. tabascum* could be as well.

Aplidium triggsense Kott, 1963
(Fig. 104)

Aplidium triggsensis Kott, 1963, p.104; 1976 (*A. triggiensis*) p. 61. Monniot, 1987, p.531.

DISTRIBUTION:

NEW RECORDS: Western Australia (Cockburn Sound WAM 23.84). South Australia (Pearson I., SAM E2574). Queensland (Heron I., QM GH5305).

PREVIOUSLY RECORDED: Western Australia (Triggs I. — AM U3923 holotype, Y1408 Kott 1963; Rottnest I. — AM Y1421 Y1428 Kott 1963; Nornalup — AM Y1405 Kott 1963). Victoria (Balnarring Beach — AM Y1427 Kott 1963; Westernport — Kott 1976). New Caledonia (Monniot 1987).

The Western Australian records are all from coastal habitats subjected to surf and turbulence, and the Westernport location is one where strong tidal currents prevail. A continuous temperate to tropical range is suggested by the record from Heron I.

DESCRIPTION

EXTERNAL APPEARANCE: One colony from Heron I. (QM GH5305) is an upright lobe, but usually the colonies are firm, gelatinous, investing sheets 0.5 to 0.6cm thick and 4 to 5cm in maximum extent. Varying quantities of sand are present in the basal half of the test but not in the transparent upper half. This strengthens the colony. The margins are irregular and reduced in thickness. Root-like projections from the base of the colony extend into and around particles of the substrate helping to anchor the colonies, which are found in rigorous, turbulent habitats. Zooids are crowded, conferring a reddish-pink colour on the preserved colonies. The living colony from Heron I. is reported to have been orange buff, with translucent test.

Circular cloacal apertures are randomly distributed over the surface. It is probable that the zooids are in double-row systems but this could not be confirmed in these crowded colonies. The posterior parts of the zooids criss-cross one another in the basal half of the colony.

INTERNAL STRUCTURE: Zooids are small, the contracted abdomen and thorax together being less than 3mm, although the thin posterior abdomen is up to twice that length. The branchial aperture is small, with a short siphon. The atrial aperture is a small, rounded, sessile opening with a small pointed or tridentate tongue from the upper border of the opening. The thorax has 12 wide longitudinal muscles and these extend the length of the abdomen. Stigmata are in 8 to 10 rows of up to 15. The stomach is short with 15 longitudinal folds. Testis follicles are in 2 longitudinal series, each of about 6 follicles.

One or 2 embryos are in the atrial cavity of specimens collected from Cockburn Sound in

January, Pearson I. in November, Heron I. in November, and Westernport (Kott 1976) and Western Australia in December. The larval trunk is 0.6mm long, and the tail is wound almost halfway around it. From each location larvae have from 7 to 14 small adhesive organs. These are on fine stalks expanding into cones at their base, and are in the mid-line around the anterior half of the trunk. Scattered epidermal vesicles arise in an arc from the lateral line on each side of the adhesive organs.

REMARKS

The species is distinguished by its firm colonies with sand in the basal half, its small zooids, 15

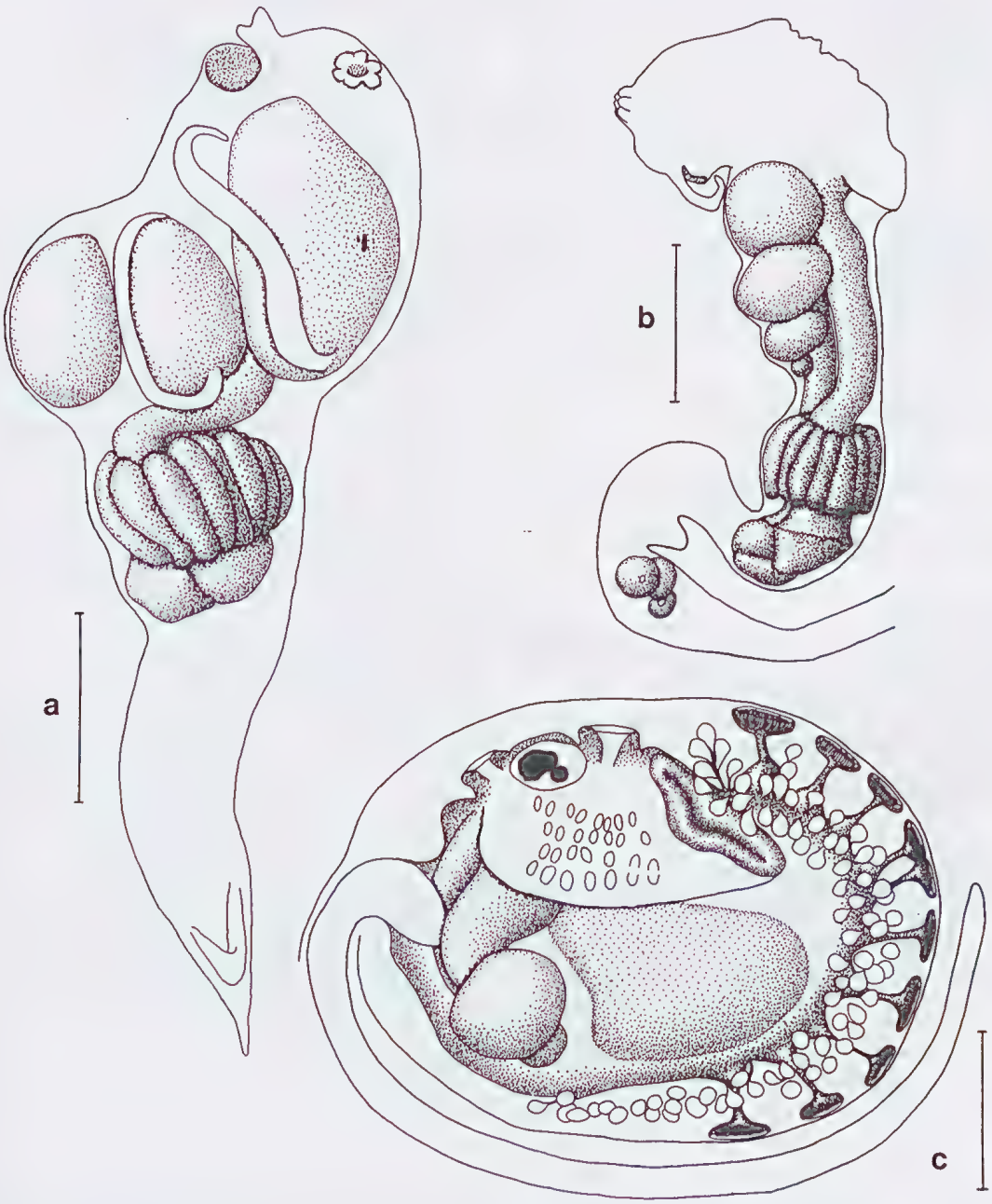


FIG. 104: *Aplidium triggsense* — **a**, **b**, zooids (WAM 23.84, QM GH5305); **c**, larva (AM Y1428). Scales: **a**, **b**, 0.5mm; **c**, 0.2mm.

stomach folds and remarkable larvae which, with 12 adhesive organs, seem adapted to make a firm adherence to the substrate in the stringent habitats from which it has been taken.

The colonies from 8cm in the lagoon, New Caledonia (Monniot 1987) are flattened lobes, joined basally, similar to the newly recorded upright lobe from Heron I.

This was previously regarded as a temperate species, but tropical records demonstrate a wider geographic range. The alternate possibility that different species are represented is not supported by the morphology of either colonies, zooids or larvae, which are all similar, with only small intrapopulation variations in size, number of stigmata, stomach folds, and adhesive organs.

Variation from the usual number (3) of adhesive organs occurs in *A. multipapillatum* Millar, 1975, from the China Sea, which has 7. It is probable that the large number in this apparently unrelated species is a convergent character, selected for in response to environmental pressures.

Aplidium uteute Monnniot and Monniot, 1987 (Fig. 105)

Aplidium uteute Monniot and Monniot, 1987, p.79.
Aplidium phortax: Kott, 1963, p. 109.
Aplidium latusexitus Monniot, 1987, p. 523.

Distribution

New Records: Queensland (Capricorn Group, QM GH1342 GH5132–48 GH5220–3 GH5313 GH5510 GH5524–5 GH5598–601 GH5610 GH5621–6).

Further Records: Queensland (Sarina — Kott 1963). Western Pacific (Solomon Is — Kott 1963; New Caledonia — Monniot 1987; French Polynesia — Monniot and Monniot (1987).

Description

External Appearance: The colonies form flat-topped cushions, to sheets fixed by a large part of the under surface, or they reduce in diameter toward the base to form flat-topped mushroom-like colonies about 1cm in maximum diameter and 0.5cm high, fixed by a small part of the under surface. The test is firm, clear and transparent in life, honey-coloured, 'rufous' (Ridgeway 1886), or colourless. It is only rarely cloudy, although it usually does become so in preservative. The living zooids, seen through the clear, transparent test, are red, 'chrome scarlet', 'buff-yellow', 'orpiment orange', 'salmon-coloured', cream with orange stomachs, or with 'orange chrome' thoraces and flesh-coloured branchial apertures, with 'geranium-coloured' or 'dragons-blood red' abdomina, and often a 'dragons-blood red' patch each side of the base of the atrial lip or between the apertures (Ridgeway 1886). Sometimes 4 lines of dark orange pigment radiate out from the branchial aperture, including one along each side of the endostyle. Embryos when these are present, are 'saturn red', 'burnt carmine' (Ridgeway loc. cit.) or maroon. In preservative the test is yellowish and translucent and the zooids white or cream. The zooids are arranged in conspicuous circular systems of 7 to 10 zooids. Sand is often present around the outer margin of the colony, but is never embedded internally.

Internal Structure: Zooids are up to 8mm long in semicontracted condition. They have large, rounded, sometimes subdivided branchial lobes and a large, fleshy, sometimes 2-lobed atrial lip from the upper border of the atrial aperture, which also has lobes around its posterior margin. Longitudinal muscles on the thorax are fine, and numerous (about 20), extending the whole length of the zooid in a wide ventral band. There are 9 to 11 rows of up to 25 stigmata in the wide thorax. The thorax is large probably exceeding the length of the posterior abdomen when it is not contracted. In preserved specimens there often is a crescent-shaped patch of greenish coagulated blood near the top of the abdomen, probably an artefact associated with the removal of the colony from the substrate.

The stomach is large and cylindrical with from 25 to 35 fine parallel longitudinal folds. The duodenal area and mid-intestine are continuous, and open into the oval posterior stomach at the base of the descending limb. A rectal valve is at the junction of the distal part of the mid-intestine and rectum at the end of the abdomen.

An ovary with up to 5 oocytes is about one-third of the distance down the posterior abdomen. The pear-shaped male follicles are posterior to the ovary, sometimes bunched but in other specimens spread out in an irregular longitudinal series. The posterior abdomen in this species is relatively short, often stumpy and only occasionally more than twice the length of the rest of the zooid.

Usually one or 2, but occasionally up to 5, embryos are in a brood pouch that projects out from, and is constricted off from, the posterodorsal corner of the thorax in zooids collected at Heron I. in May to August. The tailed larvae have a 0.65 to 0.8mm long trunk, and are deep sometimes almost spherical. The tail is wound two-thirds of the way around the trunk. Three or 4 fine,

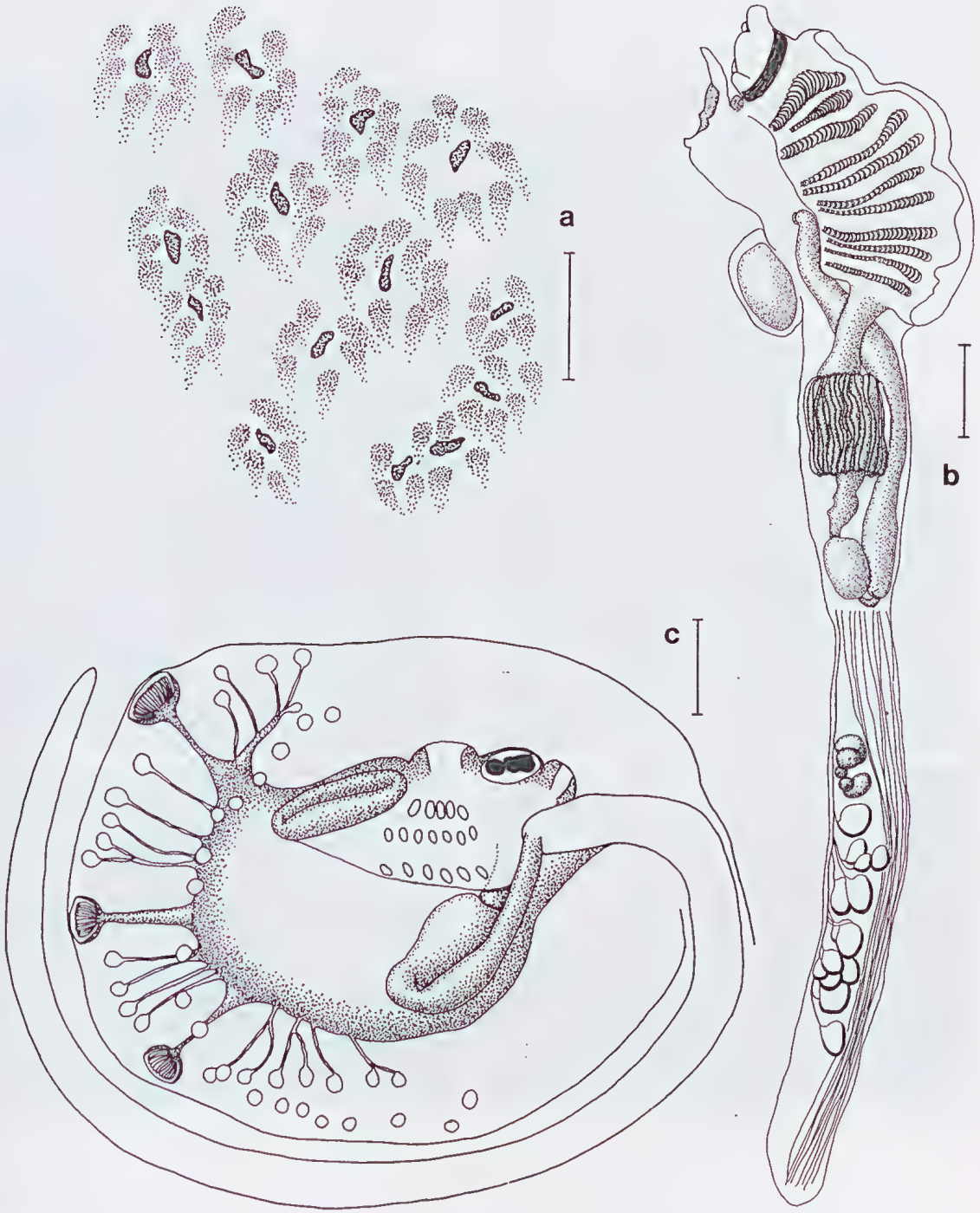


FIG. 105: *Aplidium uteute* — **a**, surface view of colony indicating systems (QM GH5134); **b**, zooid with embryos in brood pouch (QM GH5145); **c**, larva (QM GH5623). Scales: **a**, 5mm; **b**, 0.5mm; **c**, 0.1mm.

sometimes branched, stalks with terminal ectodermal vesicles extend out from the anterior mid-line in each interspace between the adhesive organs; and 20 vesicles develop in the same way from each lateral line around the anterior end of the larva. There are 3 rows of stigmata and a large ocellus and otolith in the cerebral vesicle.

REMARKS

The characteristics of this species are its transparent test, conspicuous circular systems, wide thorax, relatively long cylindrical stomach with numerous folds, postero-dorsal thoracic brood pouch, deep larval trunk with median epidermal vesicles alternating with the adhesive organs, and arc of about 20 vesicles along each lateral line. Stomachs are orange, some red pigment in the zooids, embryos and larvae are maroon-coloured.

The Australian material appears to be conspecific with *Aplidium uteute* Monniot and Monniot, 1987 from French Polynesia which has a similar stomach, large atrial aperture with the upper rim produced into a large lip, embryos incubated in a brood pouch constricted off from the thorax, red pigment each side of the neural complex, and apparently circular systems. The number of rows of stigmata are the same but unfortunately the number per row is not recorded for the Polynesian material. The number of stomach folds of the Polynesian type is said to be 50, but the number shown in Fig. 28 (Monniot and Monniot 1987) appears to be no more than 35. Monniot and Monniot (1987, Planche V-H) compared the species with a range of probably unrelated specimens assigned by various authors (Tokioka 1953, 1967a; Kott 1972, 1975; Nishikawa 1984a) to *A. pliciferum* Redikorzev, 1927 from the northwestern Pacific. *Aplidium uteute* is readily distinguished from these by many characters. However, there are others that appear to have closer affinities with which it was not compared.

Aplidium latusexitus Monniot, 1987 has circular systems, and, like *A. uteute*, red pigment patches each side of the neural gland, a large atrial aperture with a large lip, 10 rows of stigmata with up to 28 per row and lateral as well as median epidermal vesicles in the larva. Monniot (1987) has discussed its relationship with *A. multiplicatum* (*A. californicum*: Monniot 1987), but not with *A. uteute* with which it appears to be synonymous. *Aplidium uteute* is readily separated also from *A. multiplicatum* by its larvae, the form of the systems, the number of stigmata per row (i.e. the width of the thorax), and the consistency of the test.

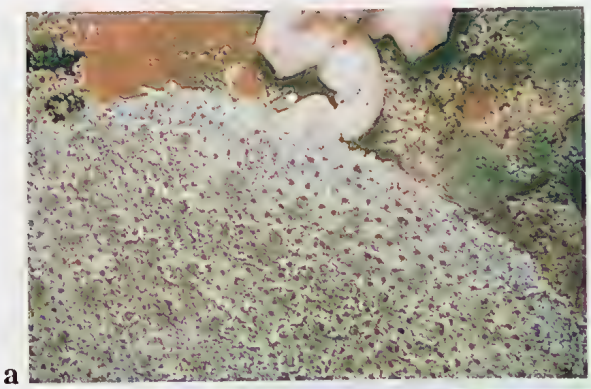
Kott (1963) assigned specimens of the present species to *Aplidium phortax* (Michaelsen, 1924) from New Zealand. However, despite similarities in the colonies and brood pouches, *A. uteute* has a wider thorax than the New Zealand species which has only 9 or 10 stigmata per row. The larva of *A. phortax* is not known.

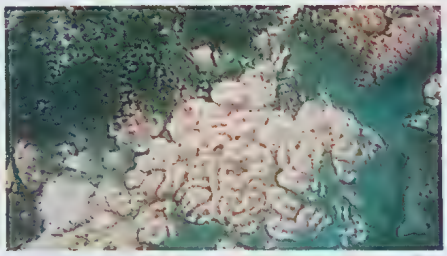
Aplidium flavolineatum (Sluiter, 1898) from South Africa (see also Millar 1962) has zooids arranged in conspicuous round to oval systems, and embryos incubated in a brood pouch slightly constricted off from the thorax. Michaelsen (1934) thought it was synonymous with *A. phortax*, however *A. flavolineatum* differs from both *A. phortax* and the present species by having embedded and encrusting sand, generally more stomach folds (although the numbers overlap, and the stomachs are a similar shape) and by usually being a red colour in life. Also, *A. flavolineatum* incubates up to 4 embryos in the brood pouch and has a larval trunk of 1mm with median ampullae and some large lateral vesicles or ampullae (Millar 1962); while *A. uteute* has a larval trunk less than 0.8mm long with more numerous epidermal vesicles.

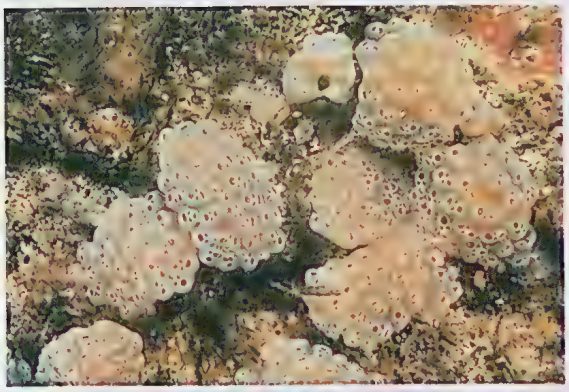
Aplidium flavolineatum: Monniot, 1987, has circular systems, brood pouch, and stomach resembling those of the present species. However the larvae, found in the single colony that Monniot described, have fewer epidermal vesicles than *A. uteute*. These vesicles, like those of *A. altarium* remain attached to the trunk epidermis. *Aplidium altarium* also has a large number of stomach folds, but is distinguished by its converging double row systems.

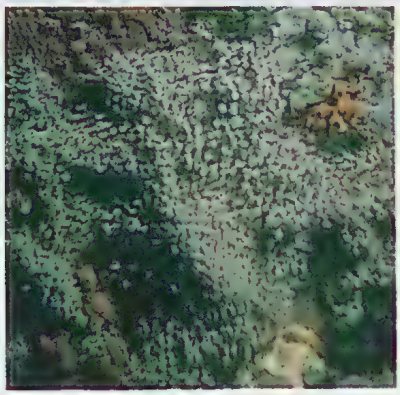
Aplidium ornatum is another species with large numbers of stomach folds, but its larvae lack the long arcs of evenly spaced epidermal vesicles that characterise the larvae of the present species.

PLATE 1: **a**, *Monniotus australis* (QM GH4147 Price I., SA). **b–d**, *Condominium areolatum* n.gen. n.sp. (**b**, QM GH4161 Taylor I. SA; **c**, **d**, QM GH5418 central Great Barrier Reef Qd 20m). **e**, **f**, *Ritterella asymmetrica* (**e**, QM GH4195 Hopkins I. SA; **f**, QM GH5445 Cape Jaffa SA). Photos: **a**, **e**, S.A. Shepherd; **b**, W.H. Sasse; **c**, **d**, **f**, AIMS Bioactivity Gp, Q66-C1723–C2457.









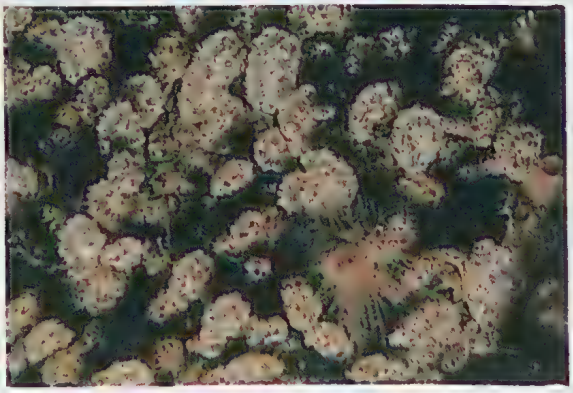


PLATE 2: **a**, **b**, *Ritterella compacta* n.sp. (**a**, QM GH2399 holotype Flinders I. SA; **b**, QM GH4177 The Gap SA). **c**, *Ritterella cornuta* n.sp. (QM GH4176 holotype Price I. SA). **d**, *Ritterella dispar* (QM G12001 Lord Howe I.). **e**, *Ritterella multistigmata* n.sp. (QM GH5463 holotype Rockingham WA). **f**, **g**, *Ritterella pedunculata* (**f**, QM G10156 George's Bay Tas. 5m; **g**, QM G10160 Phillip Bay Vict. 10m). Photos: **a**, N. Holmes FL975-PE0030; **b**, **c**, W.H. Sasse 9.4.87 7.4.87; **d**, **f**, **g**, N. Coleman AMPI 250 211 170; **e**, AIMS Bioactivity Gp Q66-C2822.

PLATE 3: **a**, *Euherdmania translucida* n.sp. (QM GH2310 Flinders I. SA). **b**, *Pseudodistoma acuatum* n.sp. (QM GH2323 holotype Ward I. SA). **c**, **d**, *Pseudodistoma australe* (QM G92 Exmouth Gulf WA). **e**, **f**, *Pseudodistoma candens* n.sp. (QM GH5462 Rockingham WA). Photos: **a**, **b**, N. Holmes FL985-PE0064; **c**, **d**, N. Coleman AMPI 76 77; **e**, **f**, AIMS Bioactivity Group Q66-C2798.

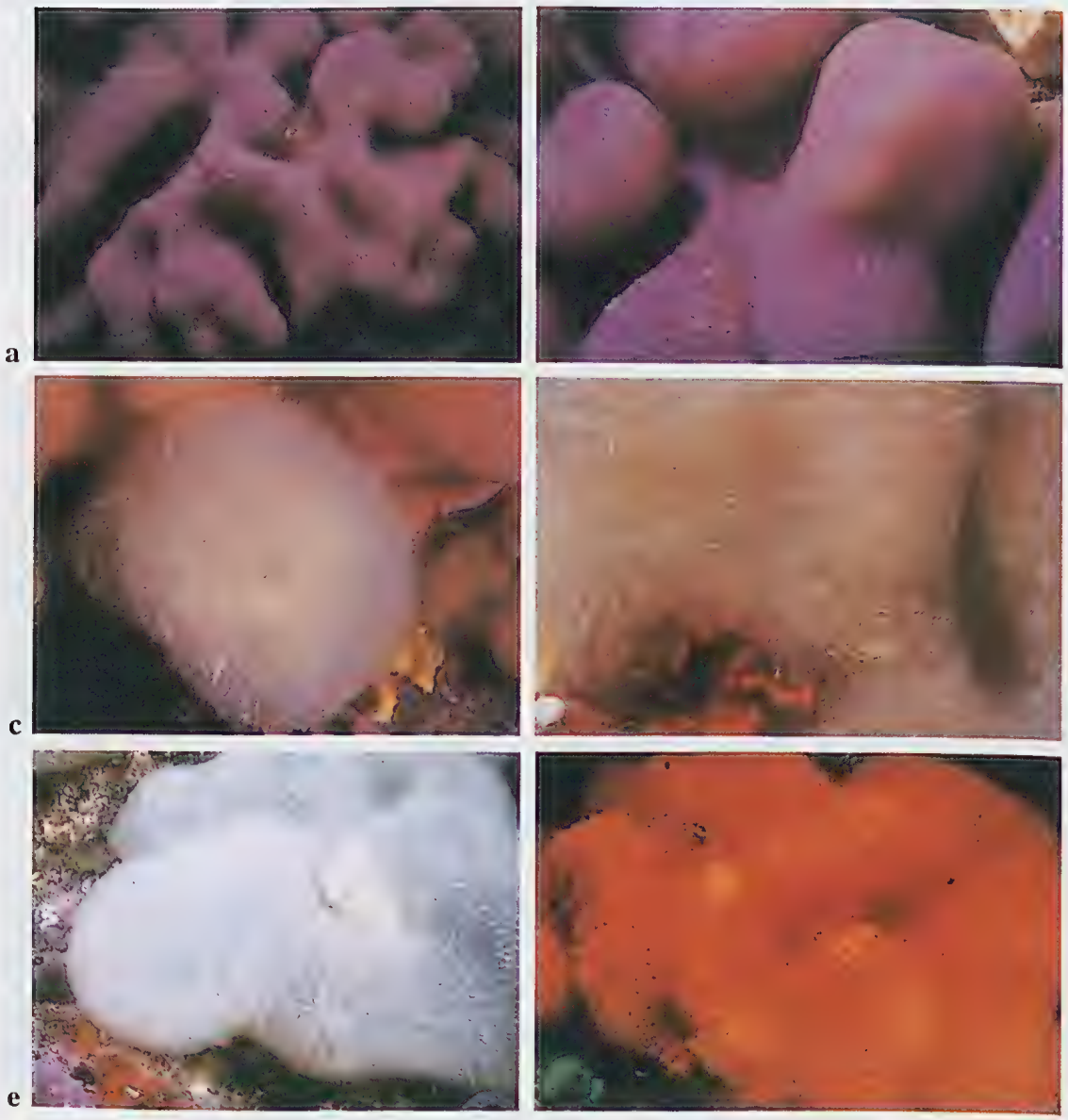


PLATE 4: **a–e**, *Pseudodistoma gracilum* n.sp. (**a**, QM G11989 Kangaroo I. SA; **b**, QM GH4158 Cathedral Rock SA; **c**, Kangaroo I. SA; **d**, QM GH4167 paratype Grindal I. SA; **e**, ? SA). **f**, *Pseudodistoma inflatum* n.sp. (QM G9472 paratype Byron Bay NSW). Photos: **a**, **c**, **f**, N. Coleman AMPI 227 223 158; **b**, **d**, W. H. Sasse 23 19; **e**, R. Kuiter 47SS.

PLATE 5: **a**, *Pseudodistoma oriens* n.sp. (Port Phillip Heads Vict.); **b–d** *Pseudodistoma pilatum* n.sp., showing colour variants (**b**?; **c**, SAM E2409 paratype Cathedral Rock SA; **d**, QM GH4140 paratype Golden I. SA). **e**, **f**, *Pseudodistoma pulvinum* (**e**, QM GH2396 holotype Ward I SA, in caves; **f**, QM GH2300 Flinders I. SA).Photos: **a**, J. Watson April 1977; **b**, R. Kuiter 54SS; **c**, **d**, W.H. Sasse 20 10; **e**, **f**, N. Holmes FL979-PE0012 FL964-PE0060.

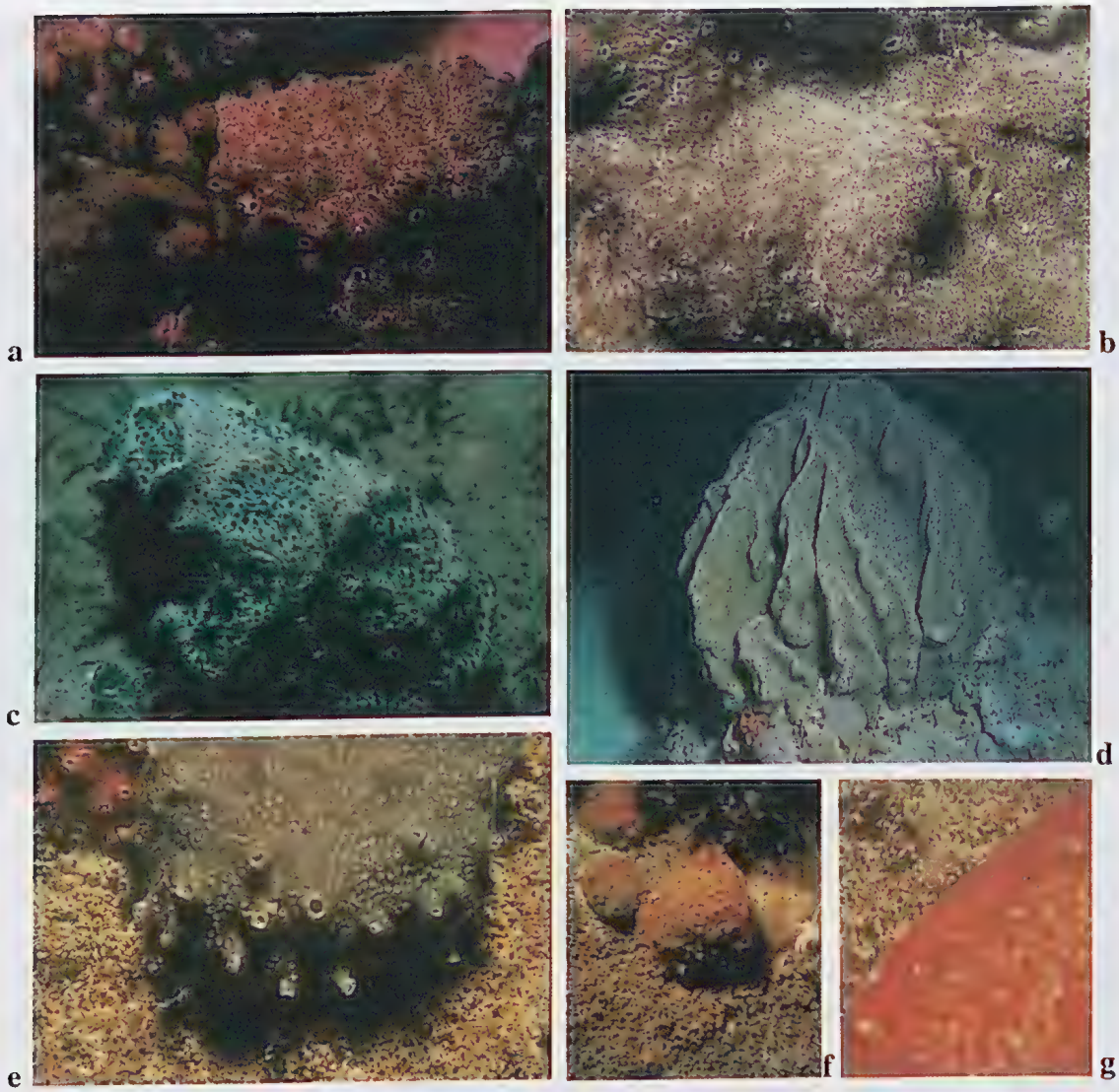


PLATE 6: **a**, **b**, *Polyclinum incrustatum* (**a**, QM GH4141 Perforated I SA; **b**, The Gap, QM GH4163). **c**, **d**, *Polyclinum marsupiale* (**c**, QM G10138 Kingston Jetty SA; **d**, QM G10175 Deal I. Bass Strait)). **e–g**, *Polyclinum nudum* n.sp. Coffs Harbour NSW, showing colour variants (**e**, QM GH5387; **f**, QM GH5388; **g**, QM GH5390). Photos: **a**, **b**, W.H. Sasse 34 3; **c**, J.E. Watson September 1977; **d**, N. Coleman AMPI 114 6.5.74; **e–g**, AIMS Bioactivity Gp Q66-C1108 -C1129 -C1131.

PLATE 7: **a**, *Polyclinum tenuatum* n.sp. (QM GH5444 Cape Jaffa SA). **b**, **c**, *Polyclinum terranum* n.sp. QM 5460 holotype Rockingham WA (**b**, distant view showing top of colony exposed on surface of substrate; **c**, close up). **d**, *Aplidiopsis mammillata* n.sp. QM GH1468 holotype Cathedral Rock SA). **e**, *Aplidiopsis sabulosa* n.sp. (QM GH4153 holotype Avoid Bay SA). **f**, *Sidneioides tamaramae* (QM G11859 South Ulladulla NSW). Photos: **a**, **b**, **c**, AIMS Bioactivity Gp Q66-C2455 -C2794; **d**, **e**, W.H. Sasse; **f**, I. Bennett 27.1.87.

PLATE 8: **a**, *Synoicum bowerbanki* (Blacknose Point Portland Vict.). **b**, *Synoicum buccinum* n.sp. (QM GH5045 holotype Marion Reef, Coral Sea). **c–e**, *Synoicum castellatum* n.sp. (**c**, QM GH5401 Exmouth Gulf WA; **d**, Great Keppel I. Qd 10m; **e**, QM GH5322 Lizard I. Qd). **f**, *Synoicum citrum* n.sp. (QM GH2294 Port MacDonnell SA). **g**, *Synoicum concavitum* n.sp. (QM GH5465 holotype King George Sound WA). Photos: **a**, J.E. Watson June 1979; **b**, **d**, N. Coleman AMPI 209 243; **c**, **e**, **g**, AIMS Bioactivity Gp Q66-C1362 -B2069 -C2889; **f**, N. Holmes PM1193-PE0073.

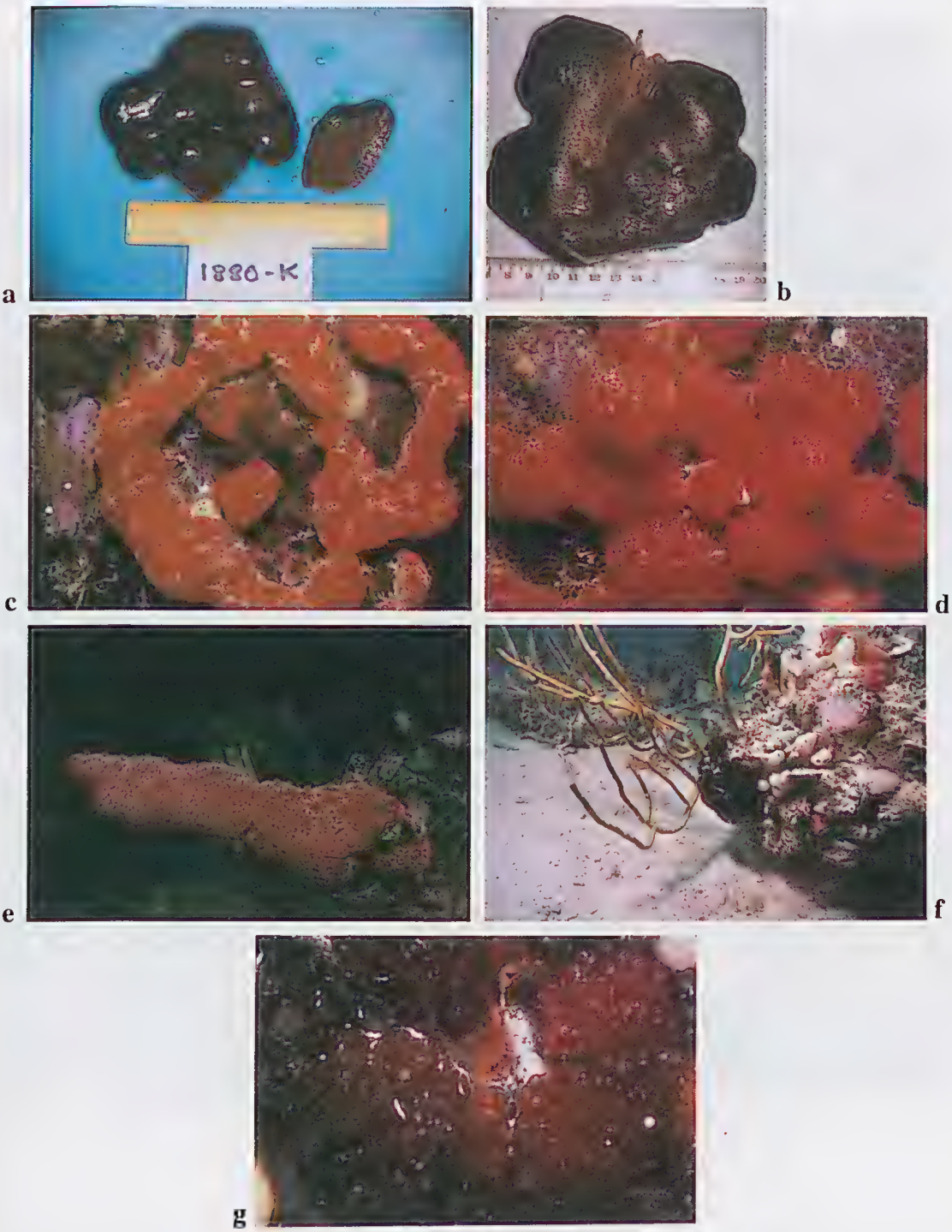


PLATE 9: **a**, *Synoicum macroglossum* (QM GH5421 Mackay Qd). **b**, *Synoicum prunum* (QM GH5394 Arrawarra NSW). **c–e**, *Synoicum sacculum* n.sp. (**c**, **d**, QM G10163 holotype Flinders Vict. 5m; **e**, Tipara Reef SA). **f**, **g**, *Synoicum suarenum* n.sp. (QM GH5377 Hardy Reef Qd). Photos: **a**, **b**, **f**, **g**, AIMS Bioactivity Gp Q66-C1880 -C1175 -C0872; **c**, **d**, N. Coleman AMPI 201; **e**, S. Shepherd 13.5.82.

PLATE 10: **a**, **b**, *Aplidium acroporum* n.sp. (**a**, QM GH5443 paratype Kangaroo I. SA; **b**, SAM E2554 holotype The Gap SA). **c**, **d**, *Aplidium altarium* (**c**, QM GH5557 Houtman's Abrolhos WA; **d**, QM GH5522 Heron I. Qd). **e**, *Aplidium bacculum* n.sp. (QM GH5434 holotype York Peninsula SA). **f**, **g**, *Aplidium brevilarvacium* (**f**, ? SA; **g**, QM GH2412 Ward I. SA). Photos: **a**, **e**, AIMS Bioactivity Gp Q66-C2445 -C2304; **b**, W.H. Sasse 14; **c**, **d**, N. Coleman AMPI 60 150; **f**, R. Kuiter 43SS; **g**, N. Holmes WD894-PE0020.

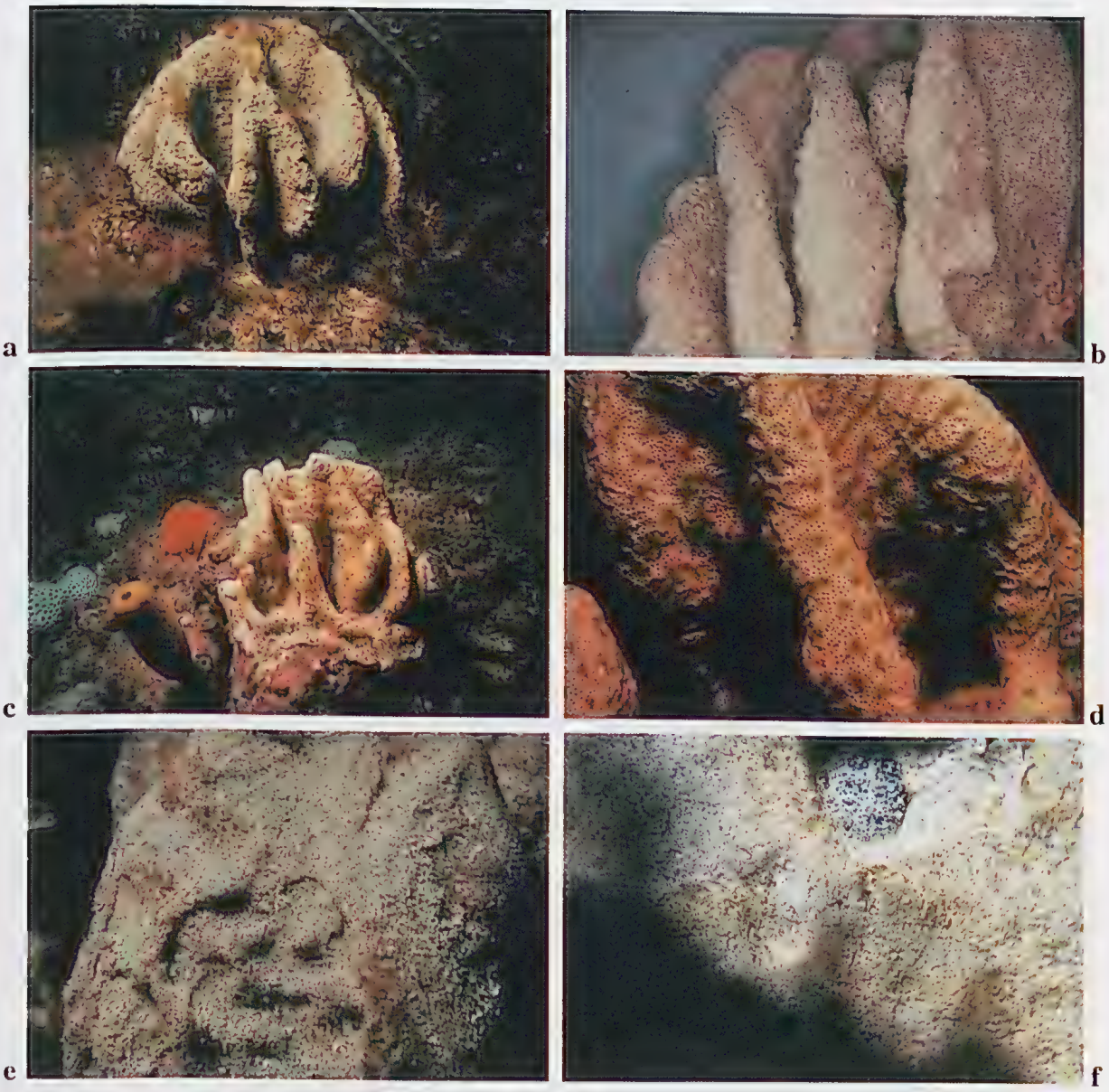


PLATE 11: **a–f** *Aplidium caelestis* (**a**, **b**, whole and part of colony respectively QM GH5430 Kangaroo I SA; **c**, **d**, whole and part of colony respectively QM GH5437 Edithburgh SA; **e**, QM GH5428 Kangaroo I. SA; **f**, Grindal I. SA). Photos: **a–e**, AIMS Bioactivity Gp Q66-C2186 -C2317 -C2184; **f**, W.H. Sasse 6.

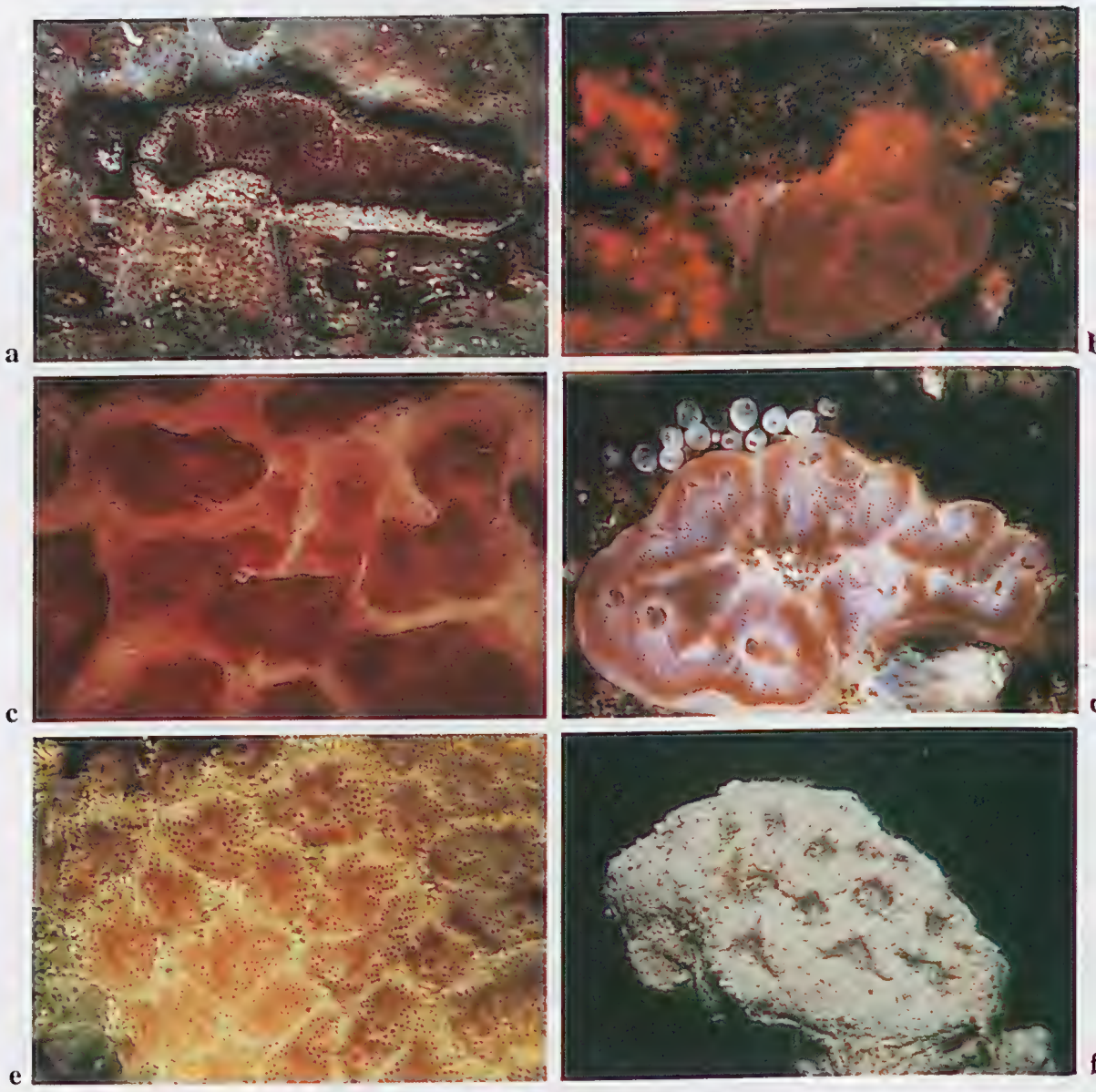


PLATE 12: **a–f**, *Aplidium clivosum* n.sp. (**a**, QM GH2417 Hotspot SA; **b**, QM GH5469 Geographe Bay WA; **c**, QM GH5447 Beachport SA; **d**, ? South Australia; **e**, QM GH5628 Jervis Bay NSW; **f**, QM GH5305 Flinders I. SA).Photos: **a**, **f**, N. Holmes HS1035-PE0008 FL792-PE0050; **b**, **c**, AIMS Bioactivity Gp Q66-C2928 -C2493; **d**, R. Kuiter SS51; **e**, N. Coleman AMPI 78.

PLATE 13: **a–c**, *Aplidium crateriferum* (**a**, Heron I. Qd; **b**, QM GH5406 Montebello I. WA; **c**, Heron I. Qd). **d–f**, *Aplidium lenticulum* n.sp. (**d**, QM GH5457 Rockingham WA; **e**, QM G9475 Carnac I. WA; **f**, Denmark WA). Photos: **a**, **c**, **e**, **f**, N. Coleman AMPI 146 197 46 119; **b**, **d**, AIMS Bioactivity Gp Q66-C1548 -C2780.

PLATE 14: **a–c**, *Aplidium lunacratum* nom. nov. (**a**, QM GH5429 Kangaroo I. SA; **b**, **c**, QM GH5446 Cape Jaffa SA). **d–f**, *Aplidium multiplicatum* (**d**, QM G10151 Wistari Reef Qd, with *Prochloron* on surface and in cloacal canals; **e**, Heron I. Qd; **f**, QM GH5361 Darwin Harbour NT). Photos: **a**, **b**, **c**, **f**, AIMS Bioactivity Gp Q66-C2185 -C2458 -C0635; **d**, **e**, N. Coleman AMPI 160, Nov. 1987.

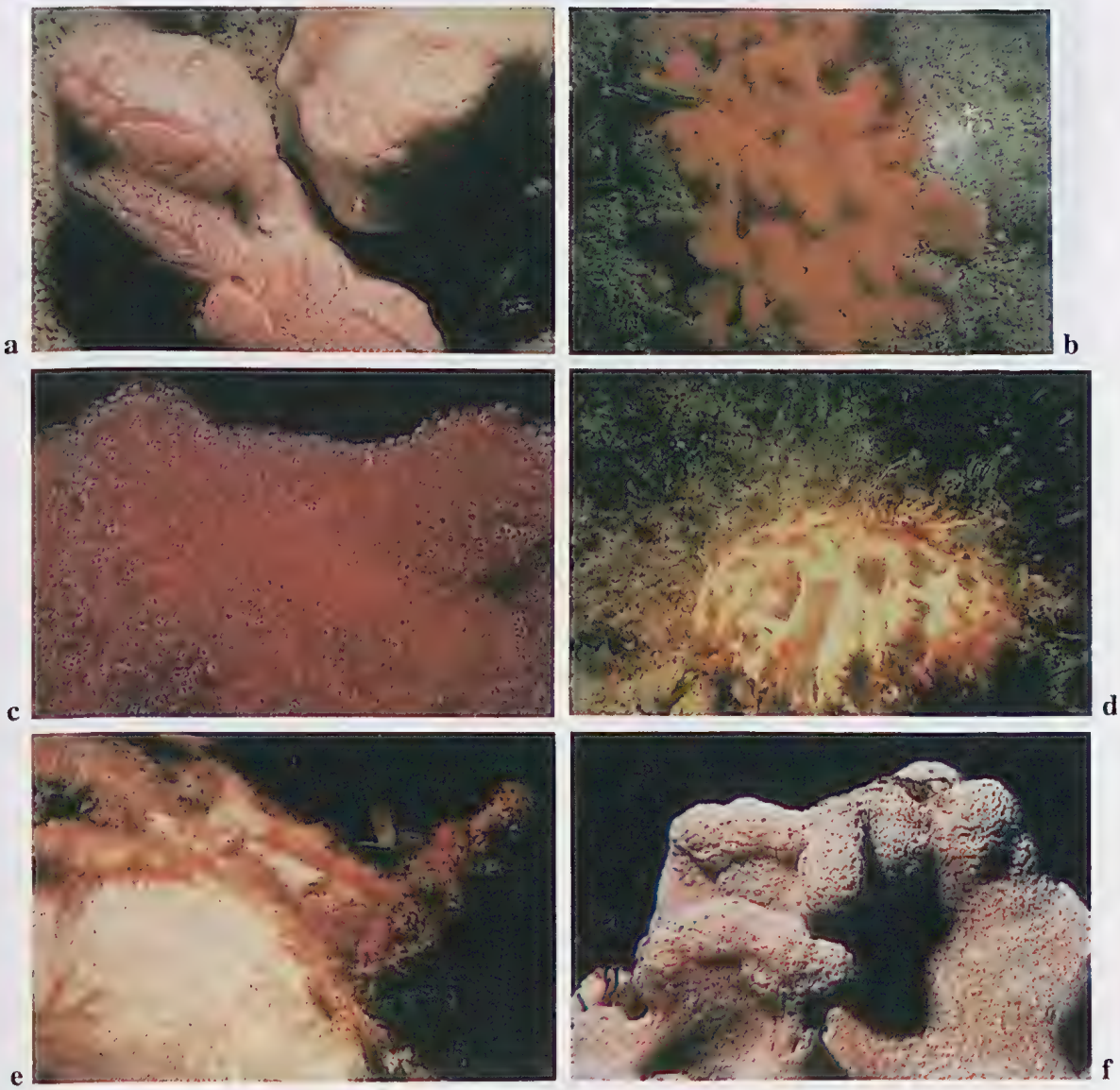


PLATE 15: **a–c**, *Aplidium opacum* (**a**, QM GH5440 Edithburgh SA; **b**, **c**, Port Hacking NSW 3m, 5m). **d–f**, *Aplidium petrosum* n.sp. (**d**, **e**, QM GH5454 Cape Jaffa SA; **f**, QM GH4165 The Gap SA). Photos: **a**, **d**, **e**, AIMS Bioactivity Gp Q66-C2376 -C2728; **b**, **c**, N. Coleman AMPI 255; **f**, W.H. Sasse 32.

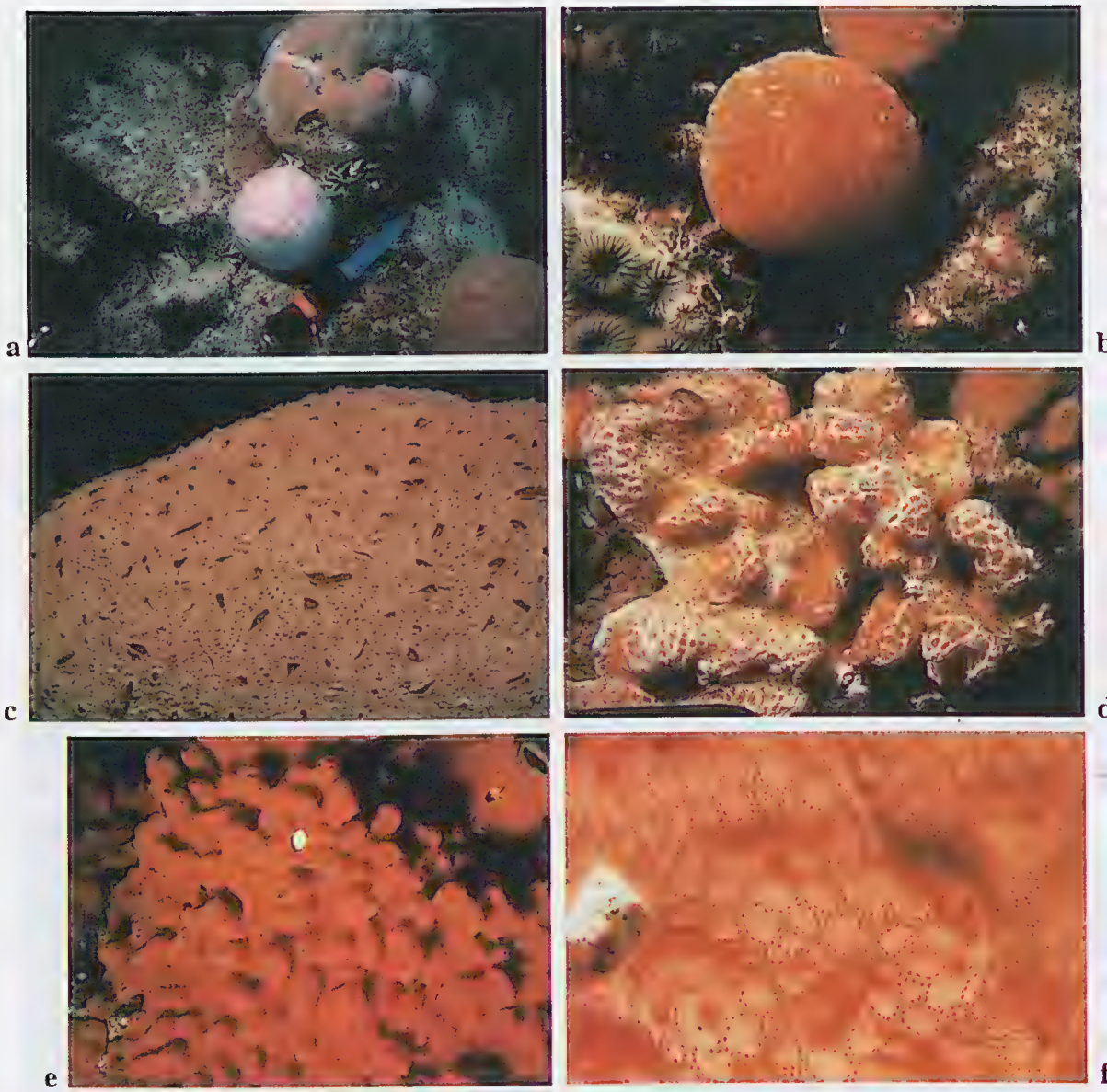


PLATE 16: **a**, **b**, *Aplidium protectans* (**a**, QM GH5378 central Great Barrier Reef; **b**, QM GH5336 far northern Great Barrier Reef). **c**, *Aplidium robustum* n.sp. (QM GH5467 holotype King George Sound WA). **d**, *Aplidium rubricollum* (QM GH4191 Golden I. SA). **e**, **f**, *Aplidium tabascum* n.sp. (**e**, QM GH5208 holotype Heron I. Qd; **f**, QM G9726 Heron I. Qd). Photos: **a–c**, AIMS Bioactivity Gp Q66-C0897 -B2177 -C2914; **d**, W.H. Sasse 14; **e**, **f**, N. Coleman AMPI 207 85.

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THE AUSTRALIAN ASCIDIACEA, SUPPLEMENT 2

PATRICIA KOTT

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Information from newly examined material and recently published reports supplements that in the continuing review of the Australian Ascidiacea (Kott 1985, 1990a, 1990b, 1992). Recorded ranges of *Sigillina fantasiana*, *Hypsistozoa distomoides*, *Polycitor obeliscus*, *Polycitorella coronaria*, *Exostoma ianthinum*, *Botryllus stewartensis*, and *Pyura rapaformis* are extended; the known depth range of *Pseudodiazona claviformis* increased; *Pycnoclavella aurantia*, *P. elongata*, *Distaplia prolifera* and *Eudistoma aureum* are now recorded from outside their type localities; new colour patterns and morphological variations are recorded for *Clavelina pseudobaudinensis*, *Pycnoclavella diminuta* and *P. elongata*; and larvae of *Pycnoclavella aurantia* and *Polycitor calamus*, described for the first time, are characteristic of their respective genera. A new species of the deep water genus *Protoholozoa* is from 7 to 15m off the southern Australian coast. A new species of *Cystodytes* has unusual spicules in a layer beneath the surface test, and one in *Polyandrocarpa*, indigenous to the central eastern Australian coast, forms colonies to a metre in maximum extent. A new *Cnemidocarpa* species has a large number of gonads, and another has only 3 branchial folds on each side.

Western Pacific species of *Ascidia* (1), *Ecteinascidia* (2), and *Pyura* (1), in the Australian fauna are found to have representatives in the component of the New Caledonian fauna previously supposed to be indigenous. The relationships and geographic range are discussed of a further 13 stolidobranch and phlebobranch species, including 4 believed to be pantropical, and abyssal *Asajirus indicus* and *Oligotrema psammites* of the Hexacrobylidae.

☐ *Ascidiacea, Aplousobranchia, Phlebobranchia, Stolidobranchia, Protoholozoa, Hexacrobylidae, Western Pacific.*

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Australian ascidians in the suborders Phlebobranchia, Stolidobranchia and Aplousobranchia (excepting the family Didemnidae) have been reviewed by Kott (1985, 1990a and 1992). Morphological, taxonomic, phylogenetic and geographic information additional to that in the first part (Kott 1985) is presented in an initial supplement (Kott 1990b). This, the second supplement, complements parts 1 and 2 (1985 and 1990a). This information is presented only when it expands known geographical range, the known morphological parameters of the taxon, or where new phylogenetic insights are available from newly examined material or recently published accounts of the western Pacific fauna, as in Nishikawa (1984, 1986), Monniot and Monniot (1987, 1990, 1991), and Monniot, C. (1987a,b, 1988, 1989, 1991a,b).

A number of Australia's tropical species are discussed here, specifically in relation to their affinities with New Caledonian populations. The ascidian fauna of the western Pacific has been relatively well studied as evidenced by the works – cited below and in Kott (1985, 1990a, 1990b) – of Sluiter, Van Name, Tokioka, Nishikawa, Kott, Vasseur, Millar, and C. and F. Monniot. From these works it is clear that Fiji, the Tokhara Is in southern Japan, Indonesia, other western Pacific locations and tropical Australia share a common fauna which sometimes extends into the Indian Ocean (see Kott 1985, 1990a, 1992). In particular, the north eastern Australian coast and the Great Barrier Reef can be said to be part of the western Pacific region.

The reports of C. and F. Monniot (1987–91) on the ascidians taken in the French 'vaste programme d'exploration' (Monniot, C. 1987a, p. 3) around New Caledonia propose new species suggesting a larger indigenous fauna than has been found previously in this or any other western Pacific location. Comparison of a number of these species, however, with related ones in tropical Australia and other western Pacific locations has shown them not to be distinct. Differences reported between New Caledonian and other populations lie within the range of intraspecific variability that is a property of all biological material. This variability is associated with age

differences, intraspecific population differences, differences between genotypes, ecological differences in growth form or pigmentation, and differences due to artefacts associated with the collection and preservation of the material. The status of morphological differences has sometimes been difficult to determine where neither intraspecific variation nor the number of specimens examined is indicated. Thus, in some, but not all, cases intraspecific differences can be confused with the genetic differences indicating isolation and speciation.

A further problem in resolving some of these problems is the relationship between apparently conspecific populations in the tropical eastern Atlantic and western Pacific — where distance and other geographic barriers would appear to preclude gene flow (see *Ascidia archaia*, *Perophora multiclathrata*, *Polycarpa aurita*, and *Cnemidocarpa areolata*, below).

Museum registration numbers are given for all examined material. Abbreviations used are AM (Australian Museum), SAM (South Australian Museum), QM (Queensland Museum), MV (Museum of Victoria). For detailed data on distribution of each taxon the registers of relevant Australian Museums must be referred to.

The following taxa are discussed below:

DIAZONIDAE
Rhopalaea crassa (Herdman, 1880)
Pseudodiazona claviformis (Kott, 1963)

CLAVELINIDAE
Clavelina pseudobaudinensis (Kott, 1976)

PYCNOCLAVELLIDAE
Pycnoclavella aurantia Kott, 1990a
Pycnoclavella diminuta (Kott, 1957)
Pycnoclavella elongata Kott, 1990a

HOLOZOIDAE
Sigillina fantasiana (Kott, 1957)
Sigillina grandissima Kott, 1990a
Distaplia prolifera Kott, 1990a
Hypsistozoa distomoides (Herdman, 1899)
Protoholozoa Kott, 1969
Protoholozoa australiensis n.sp.

POLYCITORIDAE
Cystodytes ramosus n.sp.
Polycitorella coronaria F. Monniot, 1988
Polycitor calamus Kott, 1990a
Polycitor obeliscus Kott, 1957
Eudistoma aureum Kott, 1990a
Exostoma ianthinum (Sluiter, 1909)

ASCIDIIDAE
Ascidia archaia Sluiter, 1890
Ascidia liberata Sluiter, 1887

PEROPHORIDAE
Perophora multiclathrata (Sluiter, 1904)
Ecteinascidia diaphanis Sluiter, 1885
Ecteinscidia nexa Sluiter, 1904

STYELIDAE
Cnemidocarpa amphora n.sp.
Cnemidocarpa areolata (Heller, 1878)
Cnemidocarpa intestinata Kott, 1990
Cnemidocarpa tribranchiata, n.sp.
Asterocarpa humilis (Heller, 1878)
Polycarpa contecta (Sluiter, 1904)
Polycarpa aurita (Sluiter, 1890)
Polyandrocarpa colemani n.sp.
Botryllus stewartensis Brewin, 1958

PYURIDAE
Pyura albanyensis Michaelsen, 1927
Pyura curvigona Tokioka, 1950
Pyura rapaformis Kott, 1990b
Herdmania momus (Savigny, 1816)
Microcosmus tuberculatus Kott, 1985

HEXACROBYLIDAE
Asajirus Kott, 1989a
Asajirus indicus (Oka, 1913)
Oligotrema Bourne, 1903
Oliogtrema psammites Bourne, 1903

Suborder APLOUSOBRANCHIA Lahille, 1887

Family DIAZONIDAE Seeliger, 1906

The family is distinguished from Cionidae by its relatively small thorax, long, straight, vertical gut loop, and epicardial sacs isolated from the pharynx. Further, although only 2 species of *Rhopalaea* are known to form colonies of not more than 2 zooids, other genera of the Diazonidae are colonial, replicating as do some other aplousobranchs by horizontal strobilation of the abdomen across the epicardium.

Lahille (1887) proposed a common ancestor for taxa with complete internal longitudinal branchial vessels, and accordingly included Diazonidae and Cionidae in the suborder Phlebobranchia. Most authors accepted this phylogeny until Kott (1969, 1985, 1990a) drew attention to the rela-

tionships between Cionidae, Diazonidae and other aplousobranch families, based on the presence of entire epicardial sacs and their regenerative role in the process of replication. In Phlebobranchia (but not in Diazonidae or Cionidae) the epicardial sacs are divided into minute vesicles that serve an excretory rather than regenerative function. Further, in phlebobranch ascidians (including Diazonidae and Cionidae) the gut loop is folded up alongside the pharynx while the aplousobranch gut loop, although sometimes horizontal and twisted, is always behind the pharynx. As pointed out by Kott (1985), the loss of internal longitudinal vessels occurs in parallel in all sub-orders of the Ascidiacea as zooids reduce in size with the evolution of replication and a colonial habit (see Perophoridae and Polyzoinae). The morphological relationships between Diazonidae, Cionidae and other aplousobranch (rather than phlebobranch) families is confirmed by their chemistry (see Hawkins *et al.* 1983).

Genus **Rhopalaea** Philippi, 1843

C. Monniot (1991a) believes that *Diazona* and *Rhopalaea* are indistinguishable. However, these genera are readily separated by the relatively primitive characters of *Rhopalaea* including its particularly large branchial sac, and relatively short oesophagus. Although the epicardium is used to regenerate parts of zooids, apparently the process is not one of spontaneous replication, for only 2 species of *Rhopalaea* are known to form colonies (see Kott 1990a). On the other hand, *Diazona* species have smaller thoraces, a generally longer oesophagus, and a prolific replicative capacity resulting in large colonies of numerous zooids.

Rhopalaea crassa (Herdman, 1880)

Ecteinascidia crassa Herdman, 1880, p.723.
Rhopalaea crassa Kott, 1990a, p.26 and synonymy.
Nishikawa, 1991, p.25.
Rhopalaea respiciens Monniot, C. 1991a, p.494.

REMARKS

Monniot (1991a) has suggested that species of *Rhopalaea* can be separated by the colour of the living test, the musculature and relative size of the thorax and abdomen. The significance of the colour differences that occur in living specimens of this species is not resolved. However Kott and Goodbody (1982), Kott (1990a) and Nishikawa (1991) have reported on a wide range of specimens of *R. crassa* and its synonyms from a wide range of locations, including type locations and have demonstrated similar variations in the musculature associated with contraction, and variations in the relative size of thorax and abdomen, apparently the result of growth, and regeneration of the thorax which appears to occur from time to time.

Colour differences appear partly regional, blue being the usual colour recorded for living specimens in the Philippines, while specimens with colourless, transparent thoraces with yellow, white and black markings, becoming yellow and opaque when the test is thicker, are recorded from eastern Australia (Kott 1990), Hong Kong (Kott and Goodbody 1982), New Caledonia (Monniot 1991a) and Japan (Nishikawa (1991). The colour of all specimens is lost in preservative.

Rhopalaea respiciens Monniot, 1991a falls well within the range of variation recorded for even single populations of *R. crassa*, e.g. from Heron I. (see Kott 1990a).

Genus **Pseudodiazona** Millar, 1963

Pseudodiazona claviformis (Kott, 1963) (Fig. 1)

Protopolyclinum claviforme Kott, 1963, p.72.
Pseudodiazona claviformis: Kott, 1990a, p.31 and synonymy.

DISTRIBUTION

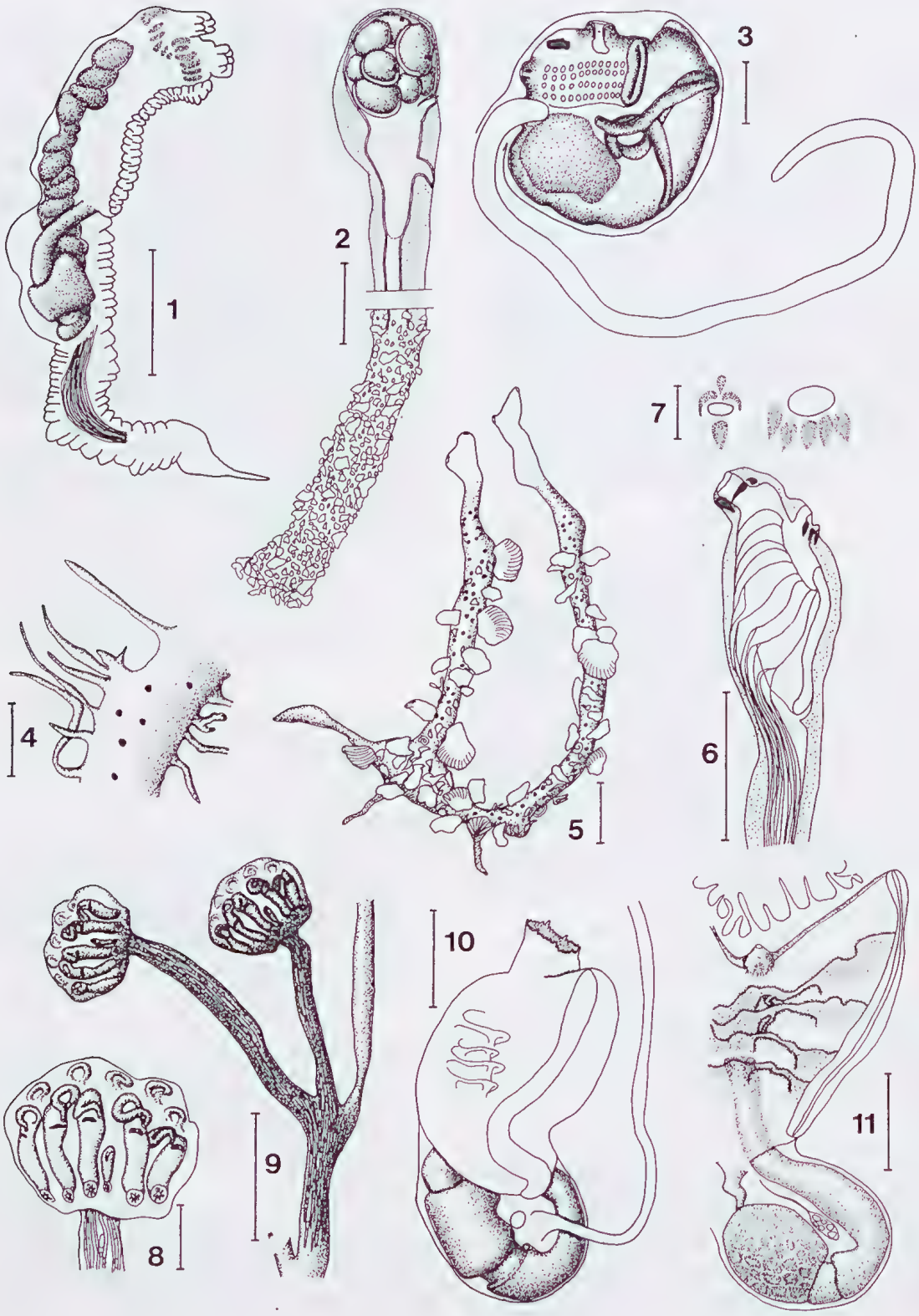
NEW RECORDS: Victoria (off Cape Everard, SAM E2460). South Australia (Spencer Gulf, SAM E2547).
RECORDED RANGE: The species is known from New South Wales and the eastern end of Bass Strait to the northern Great Australian Bight. The newly recorded specimen from Cape Everard increases the known depth range from 100 to 446m.

DESCRIPTION

The newly recorded specimens confirm the morphology of this seldom recorded species.

The specimen from Spencer Gulf retains a pattern of pale grey pigment in vertical petal shaped patches forming a ring around the base of each of the siphons.

In one specimen (SAM E2460) collected in October, the numerous male follicles are bunched in the posterior end of the zooid and eggs are lined up in a single series in the oviduct. In the other specimen gonads are not mature.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Family CLAVELINIDAE Forbes and Hanley, 1848
Genus **Clavelina** Savigny, 1816

Clavelina pseudobaudinensis (Kott, 1976)

Oxycorynia pseudobaudinensis Kott, 1976, p.54.
Clavelina pseudobaudinensis: Kott, 1990a, p.58, and synonymy.

DISTRIBUTION
NEW RECORDS: South Australia (Nuyts Archipelago, SAM E2434 E2471).
RECORDED RANGE: The known range is around the southern half of the Australian continent, from Houtman's Abrolhos to Jervis Bay (NSW).

DESCRIPTION
One of the newly recorded specimens from South Australia (SAM E2434) has a long (3cm) narrow (1.3cm diameter) stalk similar to that of *C. baudinensis* (see Kott 1990a). Otherwise the zooids are characteristic of *C. pseudobaudinensis*, with median pigment patches — one between the siphons and one at the anterior end of the endostyle. Larvae are large, with the trunk 0.9mm long (0.9cm *sic*, Kott 1990a).

Family PYCNOCLAVELLIDAE Kott, 1990
Genus **Pycnoclavella** Garstang, 1891

Pycnoclavella aurantia Kott, 1990
(Figs. 2,3)

Pycnoclavella aurantia Kott, 1990a, p.71.

DISTRIBUTION
NEW RECORD: South Australia (Thorny Passage, SW Hopkins I., SAM E2422).
RECORDED RANGE: The holotype from Franklin I. Nuyts Archipelago was the only previously recorded specimen (Kott 1990a).

DESCRIPTION
Unlike the type specimen, the vertical stalks of the newly recorded one form a sandy aggregated basal mass similar to that observed previously in *Pycnoclavella tabella* Kott, 1990a. Zooids are a gold colour in preservative.

The thoraces are turned at right angles to the long axis of the abdomen, and have a terminal atrial aperture and the branchial aperture on the side of the transparent head. Stigmata are in 6 instead of the 8 rows in the type specimens.

The newly recorded specimens, collected in October, have up to 12 embryos in the atrial cavity at the terminal end of the zooid. The larvae are large, with an almost spherical trunk about 0.9mm long with the tail wound almost once around it. There is an ocellus but no otolith, 4 rows of stigmata, and 3 characteristic deeply invaginated adhesive organs.

REMARKS
Pycnoclavella arenosa (Kott, 1972b) also has 6 rows of stigmata, but its thoraces are not turned at right angles to the long axis of the zooid, the abdomina are not free of the central common test, and the thorax is narrow (with only 20 rather than 50 stigmata per row). The tropical *Pycnoclavella detorta* (see Kott 1990a) resembles the present species in the orientation of the thorax, and in having 6 rows of stigmata. There is a difference in the number of stigmata, however, *P. detorta* having only about 24 per row.

The larva is also similar to that of *P. detorta*, having the characteristic 3 inverted tubular adhesive organs and lacking an otolith. No more than 4 embryos at a time have been found in the atrial cavity of *P. detorta*, while the newly recorded zooids have up to 12. Also the larvae of *P. detorta* have 1.7mm long trunks, longer than those of the present species (1.1mm).

The newly recorded specimens confirm the separate status of the related species *P. aurantia* and *P. detorta*.

Pycnoclavella diminuta (Kott, 1957)
(Figs. 4–7)

Clavelina diminuta, Kott, 1957, p.89.
Pycnoclavella diminuta: Kott, 1990a, p.73 and synonymy.

FIGS. 1–11: *Pseudodiazona claviformis* (SAM E2547) — 1, contracted zooid. *Pycnoclavella aurantia* (SAM E2422) — 2, zooid in test showing embryos in atrial cavity (1cm excised from oesophageal neck); 3, larva. *Pycnoclavella diminuta* — 4, section of colony stalk showing vesicles and hair-like test processes (SAM E2473); 5, part of colony (SAM E2473); 6, thorax showing pigment patches around apertures (SAM E2492); 7, detail of pigment patches around atrial (left) and branchial apertures. *Protoholozoa australiensis* n.sp. (holotype SAM E2423) — 8, head of colony showing zooid arrangement; 9, part of colony; 10, zooid from ventral surface; 11, zooid, dissected down endostyle showing transverse vessels in thorax. (Scales: 1,4,10,11 — 0.5mm; 2,5,8 — 2mm; 3 — 0.25mm; 6 — 1mm; 7 — 0.2mm; 9 — 5mm).

DISTRIBUTION
NEW RECORDS: South Australia (Nuyts Archipelago, SAM E2473; Lincoln National Park, SAM E2492).
RECORDED RANGE: The species is often encountered in benthic collections from all around the Australian coast and in the Western Pacific.

DESCRIPTION
The newly recorded colonies (SAM E2473), have their stalks aggregated together into a loose sandy mass that readily distintegrates. This mass is formed by hair-like test processes from along the stalks of adjacent zooids adhering to sand particles. The usual oily-looking spheres characteristic of this species are in the test of the stalks. It is probable that the basal sandy mass was buried in the substrate, and that only the thoraces projected above the surface.

The specimen lot SAM E2492 has unusual comma-shaped pigment patches around each smooth-rimmed aperture. In preservative these patches are a brown-orange colour. Around the atrial aperture 3 of these patches are arranged symmetrically in front of the aperture (between the siphons) and one is behind the aperture. Five patches, each with its point directed posteriorly, are in a row around the ventral border of the branchial aperture. These 5 separate patches sometimes are confluent.

Despite this unique pigment pattern, the zooids are characteristic of *P. diminuta*. Similar (but not identical) pigment patches are around the branchial apertures of specimens from Exmouth Gulf (QM GH4083: Kott 1990a, Plate 6d).

Pycnoclavella elongata Kott, 1990

Pycnoclavella elongata Kott, 1990a, p.76.

DISTRIBUTION
NEW RECORD: South Australia (St. Vincent Gulf; SAM E2418).
RECORDED RANGE: The species was previously known only from type localities amongst rocky outcrops around the Nuyts Archipelago. The newly recorded specimen is from a boat ramp at 3 to 5m.

DESCRIPTION
Thoraces are dark coloured in preservative, and naked. The stalks are aggregated together to form a basal mass of parallel, vertical sandy stalks. Zooids have 11 rows of stigmata, while the type material has 14 rows. Specimens otherwise conform with the previous descriptions of this species (Kott 1990a).

Family HOLOZOIDAE Berrill, 1950
Genus **Sigillina** Savigny, 1816

Sigillina fantasiana (Kott, 1957)

Eudistoma fantasiana Kott, 1957, p.76.
Sigillina fantasiana: Kott, 1990a, p.92.

DISTRIBUTION
NEW RECORDS: Tasmania (Break Sea I. Port Davey, QM GH5504). South Australia (Spencer Gulf, SAM E2505 E2518–9; Yorke Peninsular, SAM E2485 E2488; St. Vincent Gulf, SAM E2483 E2494; Pearson I., SAM E2537).
RECORDED RANGE: The species is known from Cockburn Sound (WA) and across the southern coast of the continent to Gabo I. off the south eastern coast. The newly recorded specimen from Port Davey, southwestern Tasmania, suggests a range around that island.

DESCRIPTION
Colonies from Tasmania are small cushions with evenly distributed blue zooids and a cloudy test. Larger sheet-like colonies from South Australia, growing along *Zostera* stalks, have almost glassy test and blue pigment around the apertures.

Zooids have a characteristically short abdomen up to 3 times the length of the thorax. A relatively long vascular stolon projects from the posterior end of the abdomen. Three embryos are lined up from the top of the abdomen to the postero-dorsal part of the thorax, where the most advanced projects from the body wall. Tailed larvae are present in February (SAM E2519), July (SAM E2494), September (SAM E2483), and November (SAM E2488 E2518)

Sigillina grandissima Kott, 1990

Sigillina grandissima Kott, 1990a, p.93.

DISTRIBUTION
NEW RECORDS: South Australia (W. Great Australian Bight, SAM E2452 E2457 E2479–81 E2545).
RECORDED RANGE: The species is known from Dampier Archipelago to the Great Australian Bight, although, so far there is a gap in the records between Cockburn Sound and Eucla (SA).

DESCRIPTION
The specimens are fleshy lobes with thick fleshy stalks about the same length as the oval head. They are a very soft, pale lemon in preservative with patches of dark pigment over the neural complex and at the anterior end of the endostyle.

There is no blue pigment in the epicardial sac as described for the type material.

Zooids and larvae are characteristically large, the larval trunk 3.8mm long with a short tail that reaches only part of the way along the ventral surface. A narrow waist is behind the 2 large adhesive organs. Three broad ampullae are on each side, at the base of the thick stalks of the adhesive organs. Larvae are present in January (SAM E2480).

Genus **Distaplia** Della Valle, 1881

Distaplia prolifera Kott, 1990

Distaplia prolifera Kott, 1990a, p.122.

DISTRIBUTION

NEW RECORDS: Western Australia, (Dampier Archipelago, QM GH5399 GH5409–10 GH5413).

RECORDED RANGE: Only the holotype colony from off Port Hedland was known previously.

DESCRIPTION

The colonies are all robust sheets with spongy test. Zooids are in circular systems, slightly depressed into the surface. They are pink in preservative. Parastigmatic vessels cross each row of moderately numerous stigmata. The vertical stomach has longitudinal striations internally but is smooth externally. The gonads are in a posterior abdominal sac.

Genus **Hypsistozoa** Brewin, 1956

Hypsistozoa distomoides (Herdman, 1899)

Amaroucium distomoides Herdman 1899, p.72.
Hypsistozoa distomoides: Kott, 1990a, p.134.

DISTRIBUTION

NEW RECORD: Tasmania (W. of Mutton Bird I., SAM E2451).

RECORDED RANGE: The species is known from the Great Australian Bight to Port Jackson New South Wales. The new record from Tasmania represents the southern limits of the known range.

Genus **Protoholozoa** Kott, 1969

Type species: *Protoholozoa pedunculata* Kott, 1969.

The genus has the long posterior abdominal stolon characteristic of the Holozoidae. Its short abdomen with the gonads and gastric vesicle in the gut loop, and its 2 to 4 transverse vessels suggest an affinity with *Sycozoa* and *Distaplia*. The arrangement of the zooids in the colony, opening separately rather than in double rows, is like another holozoid genus *Sigillina*. The colonies with long, soft, cylindrical stalks, also resemble those in other holozoid genera. The genus is separated from others in this family by its reduced branchial sac lacking stigmata.

As with all stalked, separately opening species, in this family (*Sigillina* spp.), as well as in other families (Pseudodistomidae and Clavelinidae: see Kott 1990a and 1992) the atrial apertures are directed toward the terminal free end of the colony while the branchial apertures face toward the base of the stalk. The advantages of this orientation of the apertures are discussed by Kott (1989b).

Six species are now described in the genus *Protoholozoa* (see Monniot and Monniot, 1991). *Protoholozoa pedunculata* Kott, 1969 from the Antarctic and *P. anthos* Monniot and Monniot, 1991 from off New Caledonia each have 2 transverse vessels, while *P. lilium* Monniot and Monniot, 1982 (see also Monniot and Monniot 1991) from the Antarctic and New Caledonia (sympatric with *P. pedunculata* and *P. anthos* respectively) has 3 transverse vessels as has *P. pigra* Monniot, 1974 from the Azores and *P. cantarella* Monniot and Monniot, 1985 off South Africa. Most of these species have internally ridged stomachs (except *P. anthos* and a specimen of *P. lilium*, both from New Caledonia). With the exception of *P. pigra*, the colonies are stalked, with translucent test and flat-topped heads. The long atrial lip of *P. anthos* also appears unique. However many of the other characters formerly used to distinguish species appear variable, and additional material (especially of sympatric species such as *P. lilium* and *P. pedunculata* from the Antarctic, and *P. anthos* and *P. lilium*: Monniot and Monniot, 1991 from New Caledonia) is needed to establish the range of intraspecific variation and the taxonomic significance of the number of transverse branchial vessels.

The absence of stigmata is a characteristic of most ascidian taxa from deep slope to abyssal waters from which previously recorded species of the present genus have been taken. The new species described below is the only one recorded from shallow waters.

The statement that *Protoholozoa* was the only genus of the family Holozoidae not known from Australian waters (Kott 1990a) is now known to

be incorrect, although the type location of the Australian species is off the most southerly part of the Australian continent.

The family Holozoidae is represented in Australian waters by all its known genera, including 2 indigenous ones (*Polydistoma* Kott, 1990a and *Neodistoma* Kott, 1990a). *Sigillina* Savigny, 1816, *Hypodistoma* Tokioka, 1967, *Hypsistozoa* Brewin, 1956, *Sycozoa* Lesson, 1830 and the present genus (with the exception of *P. pigra*) are known mainly from the southern hemisphere (see Kott 1990a). Only *Distaplia* is a cosmopolitan genus.

Protoholozoa australiensis n.sp.
(Figs. 8–11)

DISTRIBUTION

TYPE LOCALITY: South Australia (approximately 1km NE Margaret Brock Reef off Cape Jaffa, 7 to 15m dropoff, overhangs, caverns, coll. W. Zeidler, K. Gowlett Holmes 17.2.89, holotype SAM E2423, paratype SAM E2422).

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: The colony consists of almost spherical heads up to 5mm diameter, each at the end of the terminal branch of a branching stalk up to 1cm long. The combined length of primary, secondary and terminal branches of the stalk are about 2cm. However the available specimens are only part of a colony and the total length of the colonies could be greater. Stalks are narrow, cylindrical, about 1mm diameter, firm and translucent, with a stiff outer cuticle on the lower part.

Zooids are in a single circle, parallel with one another, around the perimeter of the head of the colony. The abdomina of the zooids are uppermost around the top of the head. The atrial apertures are at the posterior end of the thoraces opening to the exterior in a circle around the outer margin of the head just behind its terminal free end. The antero-dorsal branchial apertures are in a circle at the other end of the head, around the top of the stalk. Posterior abdominal vascular stolons extend parallel to one another along the length of the stalk, running back past the endostyle from the centre of the gut loop to enter the top of the stalk.

Vegetative zooids are in the stalk and sometimes in the head in a circle around the top of the stalk near the anterior ends of the adult zooids. However, there is no sign of more than a single circle of zooids in each head, and the vegetative zooids formed in the stalk may move up to increase the diameter of a head, and/or to form systems in developing terminal branches of the stalk.

INTERNAL STRUCTURE: Zooids are delicate and transparent, 2 to 3mm long with the gut bend slightly to the left against the posterior end of the thorax. The ventral border of the thorax is longer than the dorsum so that the short branchial siphon turns dorsally. It has fine crenellations around the rim but no lobes. Circular muscles are around the branchial and atrial apertures and short bands extend laterally from each end of the atrial aperture which is a transverse slit at the posterior end of the thorax. Twelve, short, stumpy branchial tentacles are in a circle at the base of the branchial siphon. The branchial wall consists of 4 transverse vessels attached to about the ventral one third of the parietal body wall, and free for the dorsal two-thirds of their length. They are attached to the dorsum where they cross the dorsal sinus as wide transverse membranes, but there are no dorsal languets. A few longitudinal connectives run between the transverse vessels each side of the mid-dorsal line.

The oesophagus is short, and turns to the right to open into an almost horizontal smooth walled, oval stomach. The post-pyloric part of the gut forms a smooth curve from the distal part of the stomach to the anus near the atrial aperture. As in other genera of the Holozoidae (see *Sycozoa*: Kott 1990a) a spherical gastric reservoir is in the gut loop, together with 4 or 5 immature ova. However, the gonads are not mature in the type material.

REMARKS

The type species of this genus, *P. pedunculata* Kott, 1969 (from the Scotia Sea, the South Pacific Basin and the Antarctic Peninsula at from 3000 to nearly 5000m) differs from the present species in having 2 rather than 4 transverse vessels, an internally ridged stomach, a larger head with a thick fleshy stalk and zooids in rows of about 3 down the length of the head.

Protoholozoa anthos Monniot and Monniot, 1991, and *P. lilium*: Monniot and Monniot, 1991 also have a smooth stomach, but 3 rather than 4 transverse vessels, and, in the former species, a long anterior atrial lip (an unusual feature in this genus). *Protoholozoa cantrella* Monniot and Monniot, 1985 differs in its internally ridged stomach and 3 transverse vessels.

Family POLYCITORIDAE Michaelsen, 1904
Genus **Cystodytes** Drasche, 1884

Cystodytes ramosus n.sp.
(Figs. 12–16)

DISTRIBUTION
TYPE LOCALITY: Queensland (Central section Great Barrier Reef, Haslewood I., in bay, 20m, coll. AIMS Bioactivity Group 17.10.87, holotype QM GH5374).

DESCRIPTION
EXTERNAL APPEARANCE: The colony is a knobbly mass, basically cylindrical with side branches. Each cylindrical branch is about one to 2cm diameter, to 2cm long. The colony is about 5cm in maximum extent overall.

Zooid systems open into furrows and depressions on the outer surface and circular to oval or irregular raised zooid-free elevations are scattered between the surface openings of the systems. Each system consists of a circle of up to 20 zooids, surrounding a depression (rudimentary common cloacal cavity) in the surface. This depression contains the circle of atrial apertures. The circle of branchial apertures is slightly less than 1cm in diameter.

In life, photographs show the specimens to have a smooth, translucent colourless surface layer covering brownish-pink test. The surface 2mm of test is a translucent, firm and gelatinous layer of bladder cells. It covers a layer of calcareous plate-like spicules, lying parallel to the surface of the colony. The layer is only 1 spicule thick, but the spicules overlap one another slightly around their thickened, scalloped edges. These spicules are relatively pliable, consisting of deposits of granular calcareous material, rather than the hard rigid spicules of *Cystodytes dellachiajei*. Minute brown pigment cells are scattered through the test, especially in the surface layer. In the holotype the zooids are withdrawn from the surface into the central layer of test through the layer of spicules.

INTERNAL STRUCTURE:Contracted zooids are one to 2mm long. Both the branchial and atrial apertures are 6-lobed, on cylindrical siphons, the atrial siphon larger than the branchial siphon. Strong longitudinal muscles are in the body wall. Stigmata are long, arranged in 4 rows of about 12. The gut loop is vertical, with a large, smooth-walled stomach. About 5 pear-shaped male follicles are in the gut loop.

REMARKS
The species is distinguished from *Cystodytes dellachiajei* by the layer of spicules beneath the surface bladder cells, and the absence of a capsule of spicules enclosing the abdomen of each zooid.

Genus **Polycitorella** Michaelsen, 1924

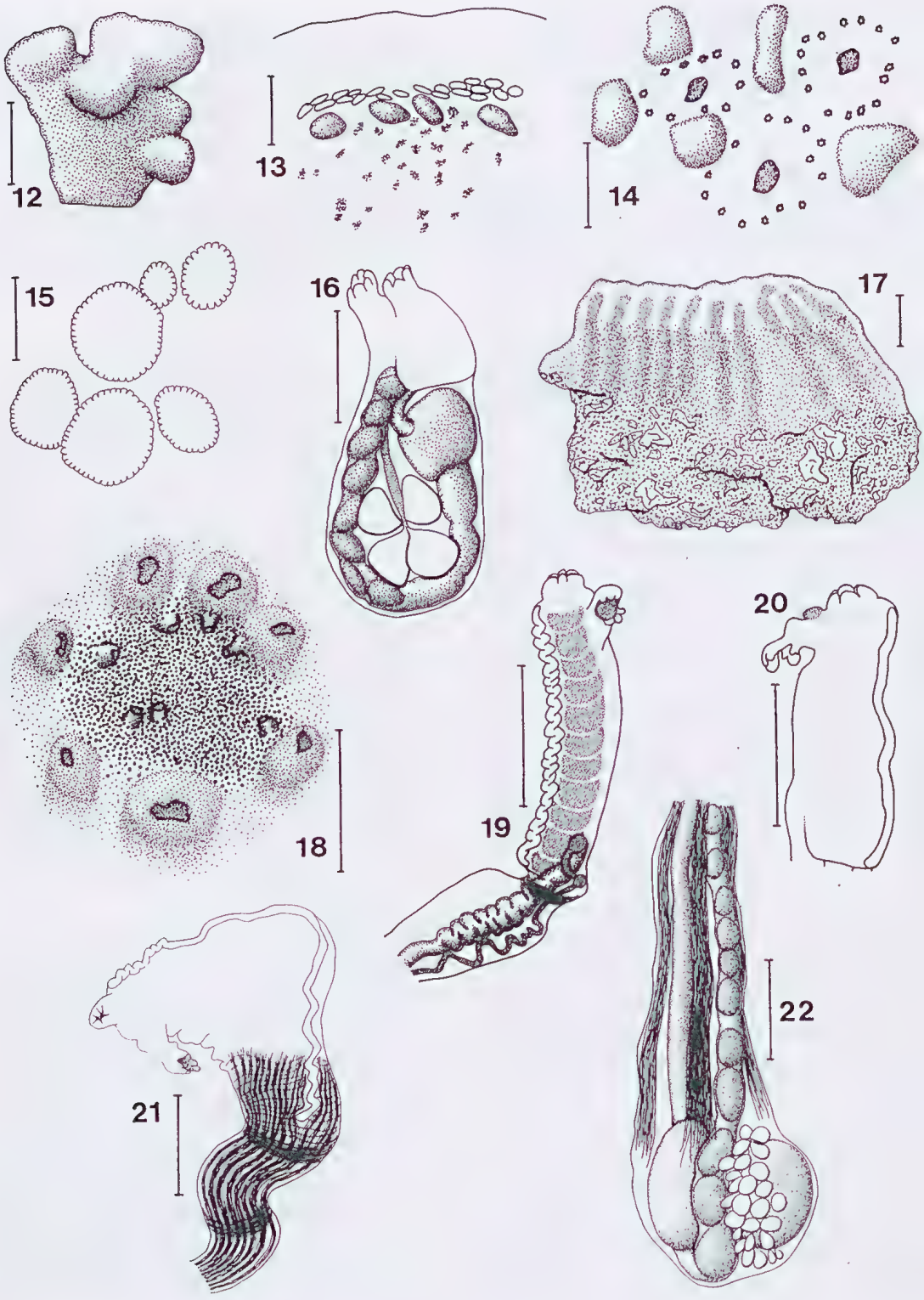
Polycitorella coronaria F. Monniot, 1988
(Figs. 17–22, 43)

Polycitorella coronaria F. Monniot, 1988, p.228. Kott, 1990a, p.184 and synonymy.

DISTRIBUTION
NEW RECORD: Queensland (Heron I. QM GH5616).
RECORDED RANGE: The species is recorded from 3 to 190m from Northwest Cape to Port Phillip Bay. The new record extends this range to the southern tip of the Great Barrier Reef.

DESCRIPTION
EXTERNAL APPEARANCE: The colony is a small thick cushion, about 1.5cm diameter and 1cm deep. Zooids are arranged in 7 circular systems of about 6 per system. Spicules are crowded in the lower half of the colony, at abdominal level. In the upper half, at thoracic level, they are present only in the centre of each circle of zooids, forming a pillar of spicules that reaches to the upper surface. The branchial apertures open around the outside of the upper margin of this white pillar, and the atrial apertures project through the upper edge and open just inside its upper margin. The external surface of the colony, both around the sides and on the flat upper surface is covered with a thick layer of bladder cells, free of spicules and pigment cells.

Pigment cells are black in the living specimen, but brown in preservative. They are crowded in the test lining the zooid compartments, and are evenly distributed elsewhere except where they are excluded by either colourless bladder cells or white spicules. Spicules are 0.025 to 0.07mm. The smaller ones are most plentiful at abdominal level around the zooids. Moderately sized ones are most frequently encountered, and the largest ones are rare. They have about 30 short pointed rays in optical section, although the smaller ones often have rounded rays. The living colony was black and white, the white circular upper surface of the pillars of spicules in the centre of each system contrasting with the rest of the upper surface where spicules are not present to dilute the black pigment cells.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INTERNAL STRUCTURE: Zooids are contained narrow vertical canals in the test, and in the present colony seem always severed somewhere along the long, narrow oesophageal neck. The rounded, slightly expanded posterior ends of the abdomina appear to have remained in place in their test compartment in the base of the colony and are not very much contracted. The anterior part of the zooids also has remained in place at the surface.

However, both the thorax and the most of the oesophageal neck is very much contracted, and it is this that appears to have caused the zooids to break apart, the abdomina remaining in the base of the colony and the apertures at the surface. The rim of the branchial aperture is divided into 6 small lobes. The atrial aperture is on a moderately long siphon. The upper rim of the opening is produced into a tongue-like lip, its tip divided into 3 round lobes. The posterior rim of the aperture also is divided into 3 lobes.

The thoracic musculature consists of about 16 narrow longitudinal bands, with very fine transverse muscles overlying them to form square meshes. Around the anterior part of the abdomen the longitudinal muscles reorganise themselves into about 8 wider bands on each side. Further posteriorly 4 wide longitudinal muscle bands encase the abdomen, but break up into separate fibres anterior to the gonads and stomach. Fine circular muscles are in one or 2 bands around the anterior part of the abdomen. These appear to be a continuation of the layer of transverse thoracic muscles onto the abdomen. Their arrangement in several bands may be due to the contraction of the longitudinal muscles. These transverse bands do not appear to have become embedded in the test, and there is not a constriction of the test between the thoracic and abdominal compartments, as there is in the large colonies of this species from southern and western Australia (see Kott 1990a).

The branchial sac is long with 13 rows of about 16 stigmata. The stomach is smooth, and located in the posterior end of the abdomen. It is obscured by the large testis consisting of numerous crowded pyriform follicles covering the dorsal side of the pole of the gut loop, and partly covered by a single large ovum.

REMARKS

Although it has been taken from Northwest Cape (Western Australia) this species has not previously been recorded from the eastern tropical coast of Australia or from any other location in the Western Pacific. The species appears to flourish in temperate Australian waters, where large colonies often are taken. This small specimen from the southern tip of the Great Barrier Reef may represent a population at the northern limits of its range. The single specimen does not appear juvenile, despite its small size, having large, mature male follicles and a large ovum. The gonads, branchial sac, circular systems, spicules, pigment cells and other features of the zooid and colony are characteristic of the species. The only significant difference appears to be the absence of a test constriction with a bundle of transverse muscle bands embedded in it between the thoracic and abdominal zooid compartments. However the transverse muscles are present outside the longitudinal ones, behind the thorax, and the fact that they have not become embedded in the test may be associated with the small size of the colony.

Genus **Polycitor** Renier, 1804

Polycitor calamus Kott, 1990
(Figs. 23–25)

Polycitor calamus Kott, 1990a, p.167.

DISTRIBUTION

NEW RECORD: South Australia (Spencer Gulf, SAM E2530).

RECORDED RANGE: The species is recorded from the Great Australian Bight and Spencer Gulf, South Australia, and from the Kurnell Peninsula (Botany Bay) New South Wales.

DESCRIPTION

The newly recorded colony is characteristic, with its long cylindrical stalk, divided into basal holdfasts that are spread out over sea grass leaves (*Posidonia*). A few epibionts are on the stalk. The expanded head has scattered spots in the surface of the preserved specimen.

FIGS. 12–22: *Cystodytes ramosus* n.sp. (holotype QM GH5374) — 12, colony; 13, section through upper part of colony showing contracted zooids beneath a layer of disc shaped spicules; 14, systems; 15, disc shaped spicules; 16, zooid. *Polycitorella coronaria* (QM GH5616) — 17, colony; 18, system from above; 19, thorax and anterior part of abdomen; 20, thorax showing atrial lip; 21, zooid showing muscle bands on abdomen; 22, gut loop and gonads. (Scales: 12 — 2cm; 13, 17 — 2mm; 14 — 5mm; 15, 16, 20–22 — 0.5mm; 18, 19 — 1mm).

The zooids have the usual long thorax and abdomen. In this colony (collected at the end of September). There are up to 9 embryos in a developmental series in the top of the abdomen. In some zooids the 2 best developed have moved up into the posterior end of the atrial cavity.

The larval trunk is up to 0.9mm long, with the tail wound about three-quarters of the distance around it. Half of the length of the trunk is taken up with a large frontal lobe which, at its anterior end, supports 3 triradially arranged, large adhesive organs. Each consists of a small everting cone in a depression at the end of a thick cylindrical stalk. The cerebral vesicle contains a large ocellus and otolith. There are 3 rows of stigmata in the larval pharynx.

REMARKS

Larvae of this species previously were unknown. Kott (1990a) suggested that since larvae were not present in the known specimens (collected in January and April) the breeding season could be restricted. The newly recorded specimens contain large numbers of relatively large embryos which appear to have been fertilised at the base of the long abdomen, and to have been developing as they move up the long stalk of the colony. This could be a lengthy process, and it suggests that sexual reproduction in this species could be an event that occurs once only during the year. The larvae, with their triradial adhesive organs and long frontal lobe, resemble the larvae of *Polycitor giganteus*, the tropical *P. annulus*, and *P. circes* (see Kott 1990a).

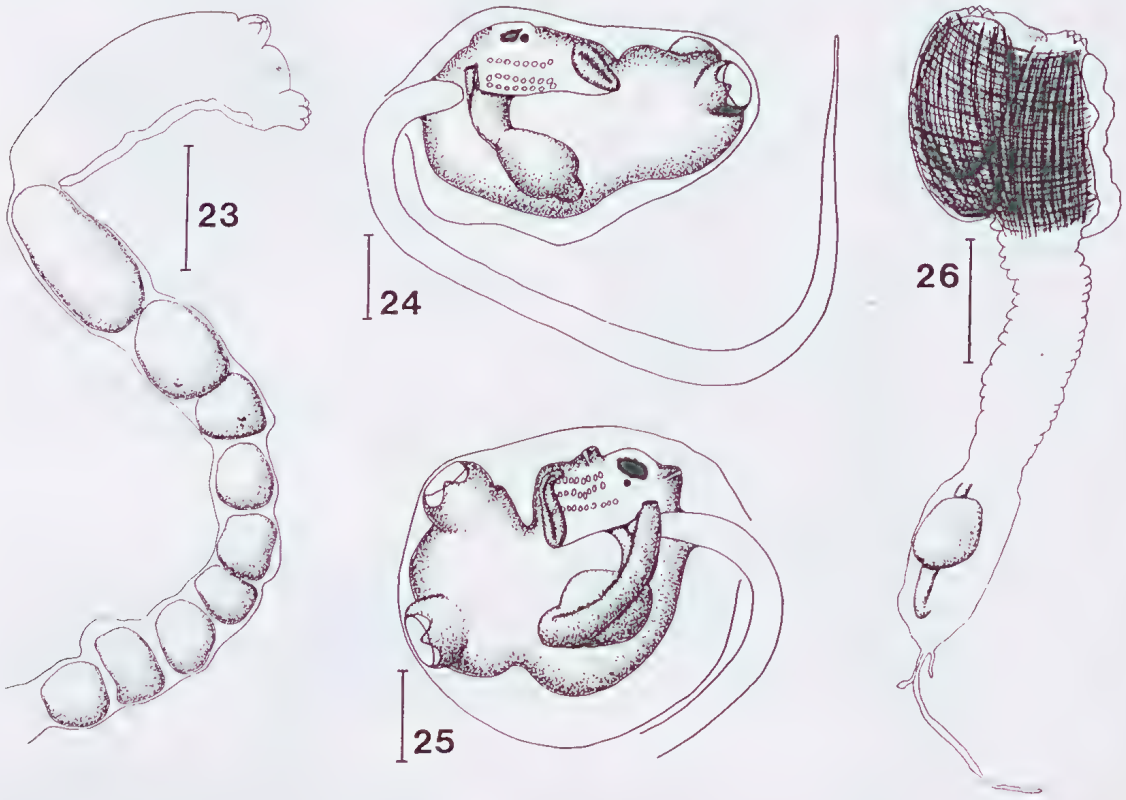
Polycitor obeliscus Kott, 1972

Polycitor obeliscus Kott, 1972b, p.171; 1990a, p.175.

DISTRIBUTION

NEW RECORDS: South Australia (Nuyts Archipelago, SAM E2543–4). Victoria (Bass Strait, MV H454).

RECORDED RANGE: The species previously was known only from its holotype from Investigator Strait. Its range is apparently restricted to the southern coast of



FIGS. 23–26: *Polycitor calamus* (SAM E2530) — 23, zooid showing embryos in abdomen; 24, 25, larvae. *Eudistoma aureum* (SAM E2538) — 26, zooid with two embryos in atrial cavity. (Scales: 23, 26 — 1mm; 24, 25 — 0.2mm).

Australia from the Great Australian Bight to Bass Strait.

DESCRIPTION

EXTERNAL APPEARANCE: The newly recorded colonies are of various shapes. The specimen from Bass Strait (at 70m) is upright, egg-shaped and fixed by its narrow base. The other colonies are fixed by a broad base (to 3cm diameter). One is a wide cone on the upper surface, but the other has a vertical margin and is flat-topped. Sand is present internally. It is absent from the surface of much of the upper part of the colony although occasionally, especially around the margins, or toward the base, some sand is present on the surface around the zooid openings. Atrial and branchial apertures open separately to the surface.

In one colony the zooids seem arranged in pairs, but there are no systems. The test is white and the zooids are reddish-orange to flesh-coloured in preservative.

INTERNAL STRUCTURE: Zooids are large and robust, with almost continuous coat of external longitudinal and internal circular muscles. The longitudinal muscles continue in 2 bands along each side of the abdomen. Stigmata are in 6 or 7 rows of about 20. The stomach, in the expanded posterior end of the abdomen, is smooth-walled. The testis follicles are clustered in a large mass on the dorsal side of the gut loop.

REMARKS

The present species is distinguished mainly by the number of rows of stigmata and the smooth-walled stomach.

Genus **Eudistoma** Caullery, 1909

Eudistoma aureum Kott, 1990
(Fig. 26)

Eudistoma aureum Kott, 1990a, p.199 and synonymy.

DISTRIBUTION

NEW RECORD: South Australia (off Eucla, 170 to 190m, SAM E2538–9).

RECORDED RANGE: The species was known only from its type locality in *Posidonia* beds in St. Vincent Gulf.

DESCRIPTION

EXTERNAL APPEARANCE: The largest colony (SAM E2538) consists of upright lobes, possibly spherical in life, but slightly laterally flattened in preservative, about 4cm diameter. It is fixed to the substrate by a narrow basal part. Internally the colony contains grey sand throughout. Sand also is present in the surface test on the lower half, which may be buried in the substrate. In preserved colonies, the surface test on the upper part of the colony, which is free of sand, is translucent and greenish black with black zooids showing through it. The arrangement of the zooids is obscure in these colonies.

INTERNAL STRUCTURE: The zooids are robust, with conspicuous muscles, about 50 internal transverse bands and 30 external longitudinal ones. Apertures are both 6-lobed. Stigmata are in 3 rows of 25 (middle row) to 30 (anterior) in each row. The dorsal end of the anterior row extends forwards along each side of the neural complex.

In the large colony taken from off Eucla, up to 2 large embryos (trunk 1.25m long) are being incubated in the atrial cavity. They have 4 lateral ampullae along each side of the median adhesive organs. However, these are crowded, the larvae are opaque and other details could not be determined. The tail is wound two-thirds of the way around the larval trunk.

REMARKS

The pigmentation in the large colony is more intense than in previously recorded specimens, which were said to have red-brown zooids in grey colonies (Kott 1990a). Possibly the colour fades in long-term preservation, for other features of both zooids and colony such as the muscular zooids, and the large number of stigmata per row, with the anterior row inclined along the mid-dorsal line, are identical.

Previously recorded colonies were said to have been yellow in life. Unfortunately the colour of the newly recorded ones is not known.

Genus **Exostoma** Kott, 1990

Exostoma ianthinum (Sluiter, 1909)

Polycitor ianthinus Sluiter, 1909, p.20.
Exostoma ianthinum: Kott, 1990a, p.234 and synonymy.

DISTRIBUTION

NEW RECORD: Queensland (Far northern Great Barrier Reef — Great Detached Reef, QM GH5726).

RECORDED RANGE: The southern limit of the recorded range of this species was previously thought to be Motupore I. New Guinea. It is known also from Palau Is, Philippines, and Bunda (Indonesia).

Suborder PHLEBOBRANCHIA Lahille, 1887

Family ASCIDIIDAE Adams & Adams, 1858
Genus **Ascidia** Linnaeus, 1767

Ascidia archaia Sluiter, 1890

Ascidia archaia Sluiter, 1890, p.346. Kott, 1985, p.26 and synonymy. Monniot and Monniot, 1987, p.92 and synonymy. Monniot, C. 1987a, p.18.

DISTRIBUTION

RECORDED RANGE: The species is known from Norfolk Is, from north of Moreton Bay and northwards up the Great Barrier Reef to New Caledonia, the Philippines, Indonesia, French Polynesia, Fiji, the Marshall Is, and the southern islands of Japan; and from the northwest coast of Australia and south to Shark Bay. The tropical Atlantic species *Ascidia corelloides* (Van Name, 1924) appears to be inseparable from it (see Van Name 1945, Tokioka 1953). Nevertheless, the Western Pacific and Atlantic populations apparently are isolated from one another, neither having a range into temperate waters.

REMARKS

Monniot and Monniot (1987) do not accept the view (Kott 1985) that *A. aperta* Sluiter, 1904 is a synonym of the present species on the grounds that it is large, up to 5cm long, with an open gut loop and with muscles on the right better developed than in the smaller specimens they have assigned to *A. archaia*. None of the characters invoked by Monniot and Monniot are outside the range of variation observed in *A. archaia*, which is one of the most common species on the Heron I. reef flat, under rubble. It is known to reach a size of 5cm in less than 6 months (see Kott 1985).

Ascidia liberata Sluiter, 1887

Ascidia liberata Sluiter, 1887, p.251. Kott, 1985, p.43 and synonymy.
Ascidia solomonensis Nishikawa, 1986, p.61.
Ascidia dorsalis C. Monniot, 1987a, p.9.
Not *Ascidia liberata*: Sluiter, 1904, p.32. C. Monniot, 1987a, p.8.

DISTRIBUTION

RECORDED RANGE: The species is recorded from Norfolk I. and the Great Barrier Reef, Indonesia (Sluiter 1887; Bay of Batavia, ZMA TU244), New Caledonia and Solomon Is.

DESCRIPTION

The species is characterised by the naked, transparent test, pointed papillae on the siphons, the fringe of minute tentacular projections along the edge of the lobes surrounding the apertures, and tranverse muscles across the dorsal surface of the generally laterally flattened, short, often triangular body, extending about half to two-thirds of the way across the right side but only about one-third of the way down the left. Short longitudinal muscles extend from along each siphon, those from the branchial siphon crossing the transverse muscles.

The red colour at the anterior end of the body in the living specimens has been referred to by Kott (1985), Nishikawa (1986) and Sluiter (1887).

REMARKS

Monniot (1987a) refers to the poor condition of the type specimen (ZMA TU244). Nevertheless it was this type specimen that Kott (1985) examined before assigning this common species to it. At the time she examined it, the characteristic papillae on the siphons, the tentacular fringe around the apertures, and the transverse muscles on the dorsal part of the right side of the body were all clearly visible. The general shape of this individual, which was figured by Sluiter (1887), closely resembles many of the more recently examined specimens.

Monniot, C. (1987a) examined and figured a specimen from the Siboga collection assigned to *A. liberata* by Sluiter (1904). Although Kott (1985) did not include it in the synonymy of *A. liberata*, Monniot believed the *Siboga* specimen to be identical with the type of *A. liberata*, and since it has characters inconsistent with *A. liberata*: Kott, 1985 he assigned the latter to a new species, *A. dorsalis* Monniot, 1987a. However, the Siboga specimen Monniot examined is not conspecific with *A. liberata* Sluiter, 1887. Its muscles, both on the right and left sides, as well as the swollen gut, the remnants of a fringe around the apertures and the foreign particles attached to the test, suggest that the Siboga specimen Monniot examined is *A. sydneiensis*.

Kott's specimens, for which *A. dorsalis* was erected, being conspecific with *A. liberata* Sluiter, 1887, *A. dorsalis* becomes a junior synonym of *A. liberata*. Similarly *Ascidia solomonensis* Nishikawa, 1986 has the characteristic features of *A. liberata* Sluiter, 1887.

Family PEROPHORIDAE Giard, 1872
Genus **Perophora** Wiegman, 1835

Perophora multiclathrata (Sluiter, 1904)

Ecteinascidia multiclathrata Sluiter, 1904, p.12.
Perophora multiclathrata: Kott, 1985, p.106 and synonymy (part, **not** *P. bermudiensis*: *pers. comm.* I. Goodbody). Nishikawa, 1986, p.30 and synonymy; 1991, p.38. C. Monniot, 1987a, p.88.

DISTRIBUTION
RECORDED RANGE: The species has a wide range in the Western Pacific from the Japan Sea (Sado), in both Micronesia and Melanesia as well as the northeastern coast of Australia, the Great Barrier Reef and Norfolk Island. *Perophora multiclathrata* also occurs on the western coast of Africa (> *Perophora africana* Millar, 1953; *fide* Nishikawa, 1986) and in the West Indies (although it is not a synonym of *P. bermudiensis*). The record from the Japan Sea is the only one outside tropical locations.

REMARKS
It is of interest that a possible junior synonym of *P. bermudiensis* (*P. fascia* C. Monniot, 1991a) occurs in New Caledonia. Although Monniot has discussed the differences of *P. fascia* from the temperate *P. hutchisoni* and tropical *P. namei*, both with jointed stolons (see Kott 1985), he has not compared the morphology of his new species with either *P. multiclathrata* or *P. bermudiensis*, species with which it has more in common. If *P. fascia* is a synonym of *P. bermudiensis*, both *P. multiclathrata* and *P. bermudiensis* are sympatric in the Western Pacific and the Atlantic.

Genus **Ecteinascidia** Herdman, 1880

Ecteinascidia diaphanis Sluiter, 1885

Ecteinascidia diaphanis Sluiter, 1885, p.168. Kott, 1985, p.90.
Ecteinascidia koumaci C. Monniot, 1987a, p.3.
Ecteinascidia ndouae C. Monniot, 1991a, p.505.

DISTRIBUTION
RECORDED RANGE: The species is known from northern New South Wales, Great Barrier Reef, Northern Australia, Palau Is, Indonesia, and New Caledonia.

REMARKS
Monniot has compared the New Caledonian material with *E. hedwigiae* Michaelsen, 1918 from the coast of Natal, and with the Western Pacific *E. diaphanis*. The latter, on geographical grounds is a more likely taxon to occur in New Caledonia. Differences between *E. diaphanis* and the 2 species from New Caledonia, viz. *E. koumaci* and *E. ndouae*, appear to be either the result of intraspecific variation, or artefacts such as muscle contraction. They include variations in the red or pink-orange pigmentation at the anterior end of the zooids, which forms rings around the siphons, and sometimes spots as well (see Kott 1985). In *E. ndouae* C. Monniot, 1991a, the colour is described as yellow-gold.

Ecteinascidia koumaci Monniot, 1987a is distinguished from *E. diaphanis* by the interval between the band of transverse muscles behind the atrial siphon and the siphonal muscles. This is affected by contraction of the longitudinal muscles along the length of the siphon. The membrane between the dorsal languets, also said to distinguish the species, is not always present (Monniot, C. 1987a). There seems no valid justification for the assignation of *E. koumaci* and *E. ndouae* to species distinct from *E. diaphanis*.

Ecteinascidia nexa Sluiter, 1904

Exteinascidia nexa Sluiter, 1904, p.11. Kott 1985, p.94 and synonymy. Nishikawa, 1986, p.42.
Ecteinascidia aequale C. Monniot, 1987a. p.5.
Ecteinascidia imperfecta: Nishikawa 1984, p.42.

DISTRIBUTION
RECORDED RANGE: The species is recorded from Lord Howe I., the northeastern Australian coast and the Great Barrier Reef, Solomon Is, Indonesia, Philipines, Fiji, Tokhara Is, the Indian Ocean (Sri Lanka), and now from New Caledonia.

REMARKS
C. Monniot (1987a), comparing *E. aequale* with *E. nexa*, was unable to reconcile the descriptions of Kott (1985) and Nishikawa (1986). However, there are not significant differences in these accounts. The species is readily characterised by its muscles, cloudy body wall in preservative, smooth stomach, duodenal and posterior stomach enlargements in the gut loop, hemispherical mass of male follicles and usually yellow colour in life. All of these characters are referred to by both Nishikawa (1986) and Kott (1985).

Ecteinascidia nexa has a range of orientations of the sessile to stalked zooids and a variety of primary and accessory stolons attaching them to the basal stolons or to one another. Apertures are, respectively, terminal and halfway along the

body, sometimes sessile, but usually on conical siphons when living. Kott (1985) describes the preserved zooids as flaccid and distorted, cloudy in preservative, with numerous blood cells. Nishikawa (1986) refers to the 'lustreless' free surface with pale yellowish spherules densely distributed in the body wall. Similar body muscles are described (in some detail) by Kott (1985) and Nishikawa (1986). Stigmata are in 19 (Kott 1985) or 20 (Nishikawa 1986) rows, and there are from 14 to 24 longitudinal vessels on one side of the body.

Both authors, independently, examined the types of *P. hornelli* Herdman, 1906, and proposed its synonymy. Nishikawa (1986) also examined the type of *E. nexa*.

The branchial processes on the prepharyngeal band figured by Kott (1985, fig. 39b) only occur in the most robust zooids and are not characteristic of the species, nor was it suggested that they are.

Ecteinascidia aequale C. Monniot 1987a from New Caledonia appears to fall within the range of variation reported for *E. nexa*.

Suborder STOLIDOBRANCHIA Lahille, 1887

Family STYELIDAE Sluiter, 1895
Subfamily STYELINAE Herdman, 1881
Genus **Cnemidocarpa** Huntsman, 1912

Cnemidocarpa amphora n.sp.
(Figs. 27–31)

DISTRIBUTION

TYPE LOCALITY: South Australia (Sir Joseph Banks Group, North Point, Marum I., 200m offshore in sand, rubble, *Posidonia*, 7m, coll. W. Zeidler 13.1.84, holotype SAM E2531; Sir Joseph Banks Group, W. Partney I., Partney Shoal Reef, rubble, sand, *Posidonia*, 5–15m, coll. W. Zeidler and K. Gowlett Holmes 21.8.86, paratypes SAM E2536.

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are club-shaped, with an expanded body, rounded anteriorly and posteriorly continuous with a thick, cylindrical stalk about the same length as the body. The branchial and atrial apertures are directed away from one another in opposite sides of the anterior end of the body, the branchial siphon almost terminal, and the atrial one on the dorsal side.

The available specimens are contracted, and behind the large, naked lobes of each aperture is a collar or band of wrinkled test. When the animal is relaxed it is probable that these disappear, and that the siphons are long, projecting out like horns from the anterior end of the body.

Sand adheres to the anterior part of the body around the base of the siphons, and to the fine hairs around the base of the stalk. The hairs aggregate together to form a sandy holdfast. The test is transversely wrinkled over most of the surface. It is particularly thin on the base of the stalk where it is surrounded by the sandy holdfast.

INTERNAL STRUCTURE: The body wall is red, shiny and muscular. Posteriorly it is extended into an inflated stolon which projects down into the stalk. Anteriorly the two siphons are relatively long, the branchial siphon directed obliquely away from the substrate, the atrial one curved over to the side toward the substrate. Attenuated body muscles are confined to the anterior part of the stolon, which is thin-walled and hollow in its distal part. The hollow may be part of the haemocoele, as it does not appear continuous with the atrial cavity, being separated from it by a thin membrane.

Longitudinal stripes line the siphons, and numerous fine branchial tentacles surround the base of the branchial siphon. The dorsal tubercle is a particularly large cushion with a double spiral slit, both horns rolled in, and directed either to the left or anteriorly. A large dorsal ganglion occupies the space between the base of the 2 siphons in these contracted specimens.

The branchial sac has 4 low folds on each side of the body, with crowded internal longitudinal vessels arranged according to the formula DL0(18)2(10)3(12)3(10)2E. About 4 stigmata are in meshes in the interspaces, and more are between the endostyle and the first longitudinal vessel on each side.

The gut loop is simple, and vertical, its pole compressed into the V of the posterior end of the body where, in these contracted specimens, it projects slightly into the top of the stalk. The oesophageal opening is halfway down the dorsal side of the pharynx. The oesophagus is short, the stomach long with parallel internal longitudinal folds. The stomach and post pyloric part of the intestine (proximal to the pole of the gut loop) are of about equal length. The rim of the anal opening (at the base of the atrial aperture) is deeply divided into 16 rounded lobes. On each side, up to 10, crowded, parallel gonads lie horizontally (at right angles to the long axis of the body). They

consist of a double rows, each row of about 10 large testis follicles, beneath a long ovarian sac.

A very short oviduct is at the dorsal end of each ovary. The short vas deferens opens on top of the female duct. Irregular, upright endocarps are crowded along the dorsal one third of each side of the atrial cavity (between the dorsal ends of the gonads, and dorsal to them).

REMARKS

Both *Cnemidocarpa floccosa* (Sluiter, 1904) and *C. completa* Kott, 1985 have a similar number of cnemidocarp gonads on each side of the body as the present species. The former tropical species is rounded posteriorly, while the present one narrows to its stalk; the gonads lie vertically, parallel to the long axis of the body in *C. floccosa*, rather than at right angles to it as in *C. amphora*; and the gut loop in the present species lies vertically, extending back from the oesophageal opening, while that of *C. floccosa* curves anteriorly around the ventral margin of the body. *Cnemidocarpa completa* Kott, 1985 is known from temperate waters, although not from South Australia. It also is distinguished from the present species by the curve of the gut loop around its posterior ventral border, the absence of a dorsal band of endocarps, the long stomach, and the loose attachment of gonads to the body wall.

Cnemidocarpa areolata (Heller, 1878)

Styela areolata Heller, 1878, p.26.

Cnemidocarpa areolata: Kott, 1985, p.122 and synonymy. **Not** Monniot, 1983, p.451 (< *C. legali* Gravier, 1955).

Cnemidocarpa valborg Monniot, 1988, p.193; 1991b, p.27 (part, ? not specimen from Dumbéa). **Not** Monniot and Monniot, 1984a, p.577 (< *C. legali* Gravier, 1955); ? 1991, p.400.

Cnemidocarpa irene: Nishikawa, 1991, p.96 and synonymy.

DISTRIBUTION

RECORDED RANGE: The species is known from all around the Australian coast, from Sri Lanka, and the western Pacific to the Marianas, Fiji, Japan and Hong Kong (see Kott 1985). The newly recorded specimens from New Caledonia (Monniot 1991b) are consistent with other records from the western Pacific.

REMARKS

Monniot and Monniot (1984a, p.577), having examined the type specimen of *C. areolata* (from Sri Lanka) found that its vas deferens was divided and that it opened by 'unbouquet de papilles'. Comparing its gut loop with Herdman's figure of *C. areolata*: Herdman, 1906 (Pl. 4, Fig. 24), Monniot and Monniot assume that Herdman's specimens, also from Sri Lanka, are conspecific with the holotype of *C. areolata*, and separate from the (principally western Pacific) specimens assigned to *C. areolata* Heller, 1878 by various authors (see Nishikawa 1991). Monniot and Monniot (1984a, p.577) contend that 'La synonymie certaine de cette espèce est restreinte au type de l'espèce et à l'échantillon de Herdman'. The specimen recorded by Nishikawa (1991) as 'C. Monniot's collected from India' apparently is part of the type of *C. areolata* Heller, 1878 'mounted on a glass slide' (see Nishikawa 1991, p.97). Neither Monniot and Monniot (1984a) nor Monniot (1988, 1991b) refer to the examination of Herdman's specimens, and there is no record that these have the remarkable, and possibly abnormal, replicated openings of the male ducts which they found in the type. Apparently the synonymy of Herdman's specimens with the type is based entirely on the curvature of the gut loop reported by Herdman (1906, pl.4, fig. 24). The curve of the gut loop is variable in the large sample of examined specimens from Australia (Kott 1985), Japan (Nishikawa 1991) and New Caledonia (Monniot 1988). Further, its curvature varies according to the curvature of the body, influenced party by its state of contractions, and by the size and shape of the adhering surface. The curvature of the gut loop is not on its own a reliable enough character to determine the relationships of the Sri Lankan specimens to one another and to others from the Indo-West Pacific. These relationships will be resolved only when the status of the unusual opening of the vas deferens (known in the one, albeit type, specimen) is established.

Cnemidocarpa valborg: Monniot and Monniot 1991 from 300 to 500m off New Caledonia has different gut loop, branchial sac and endocarps from the present species, and does not appear conspecific. Similarly, the specimen from Dumbéa (Monniot 1991b) with ducts turned ventrally does not appear to belong to this species.

The specimens from the Atlantic (Monniot 1983; Monniot and Monniot 1984a) lack the characteristic yellow and red stripes lining the siphons of living specimens, which turn to black in preservative; the gut loop is narrow, the limbs parallel to one another with endocarps in an irregular row (rather than being bunched together in the open pole of the loop (as they are in *C. areolata*);

the stomach lacks the numerous, regular parallel folds of *C. areolata*; and the posterior gonad on the left is much more branched, or it does not curve over the anterior pole of the gut loop, as in *C. areolata*. Although there are certain similarities in the morphology of these two species, they do not seem sufficiently close to justify their synonymy, especially where there is no reasonable geographic basis for gene flow between them.

Cnemidocarpa intestinata Kott, 1985

Cnemidocarpa intestinata Kott, 1985, p.128.
Not *Cnemidocarpa* aff. *intestinata*: Monniot and Monniot, 1991, p.401.

REMARKS

This species, recorded from northern and north-eastern Australia, is well characterised by its hollow conical overlapping spines (Kott 1985 Fig. 50d), large numbers of stigmata (15) in the meshes between the folds, a narrow gut loop, a gonad directed posteriorly in the second gut loop, and clumps of male follicles constricting the ovarian tubes at regular intervals along each side. Endocarps are not present.

The specimen from 700m depth off New Caledonia (Monniot and Monniot 1991), believed to have affinities with *C. intestinata*, shares only one of these characters — viz. the lack of endocarps. It does not appear to be related in any way.

Cnemidocarpa tribranchiata n.sp.
(Fig. 32–35)

DISTRIBUTION

EXTERNAL APPEARANCE: South Australia (Encounter Bay, Seal Rocks, with bryozoan *Hornera foliacea*, 15m coll. N. Holmes 24.8.88, holotype SAM E2533; Willunga Reef, low tide, coll. I.C. Kowanka 23.11.76, paratype SAM E2534.

FURTHER RECORDS: None.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are upright and oval, about 2cm long, with fleshy, 4-lobed, sessile apertures, the branchial terminal and the atrial about halfway down the dorsal surface. Irregular extensions of the basal test fix the animal to the substrate. The test is white, translucent and moderately thick and firm. The surface is slightly rough, and has patches of epibionts and shell and sand particles attached here and there.

INTERNAL STRUCTURE: The body wall has strong longitudinal muscle bands radiating from each siphon and crossing one another over the sides of the body. About 15 are from the atrial siphon and 12 from the branchial siphon. They branch into fine bands forming a delicate inconspicuous network on the postero-ventral part of the body. Circular muscles are around each siphon. A long neural ganglion is between the siphons.

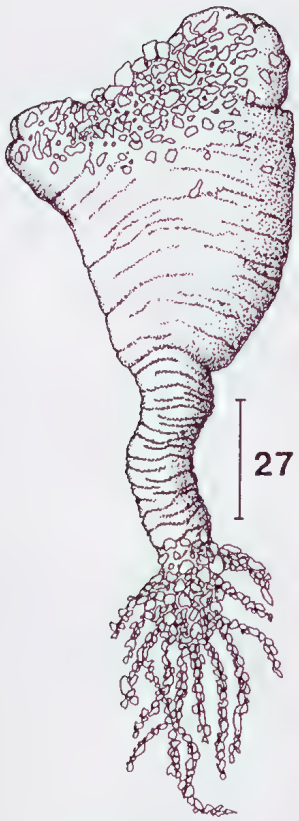
The simple branchial tentacles (about 40) are of various sizes and alternate with rudimentary ones. The dorsal lamina is wide and plain-edged. A long neural ganglion is between the siphons. The dorsal tubercle is a circular slit with a large C-shaped opening, the open interval directed anteriorly.

Three broad, but not overlapping folds are present on each side of the pharynx. Internal longitudinal vessels are thick and project into the pharynx. They are arranged according to the formula E3(13)3(12)2(13)ODL. They are not crowded, either on the folds or in the interspaces, there being 8 stigmata per mesh between the folds and 6 per mesh on the folds.

The gut loop is long and narrow, curving at least halfway around the postero-ventral curve of the body. It is open at the pole where it encloses a flat-topped endocarp which is lobed around its margin. The stomach occupies about three-quarters of the ascending limb of the gut loop. It has 11 parallel, slightly oblique folds. These flatten out at its pyloric end, which tapers gradually to the intestine. The oesophagus is short and narrow. The anus is visible through the open atrial aperture. Its margin is divided into 5 shallow lobes.

Two gonads are on each side of the body, converging toward the atrial aperture. The ovarian tubes are sinuous, the curves giving an impression of irregular lobes along each side, an impression that is emphasised by the presence of an endocarp on each outer curve. Crowded testis follicles are in 2 rows beneath each ovary. On the left side of the body the posterior gonad is curved into the secondary gut loop, and the anterior one

FIGS. 27–35. *Cnemidocarpa amphora* n.sp. (27, paratype SAM E2536; 28–31, holotype SAM E2531) — 27, 28, external appearance; 29, body removed from test showing extension into stalk; 30, internal organs; 31, lateral view of gonad. *Cnemidocarpa tribranchiata* n.sp. (holotype SAM E2533) — 32, external appearance; 33, body removed from test; 34, dorsal tubercle and anterior part of dorsal lamina; 35, internal organs on left side. (Scales: 27–29, 31, 32 — 5mm; 30, 34, 35 — 1mm; 33 — 2mm).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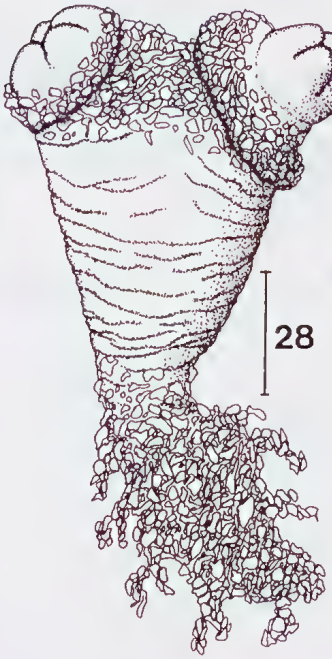
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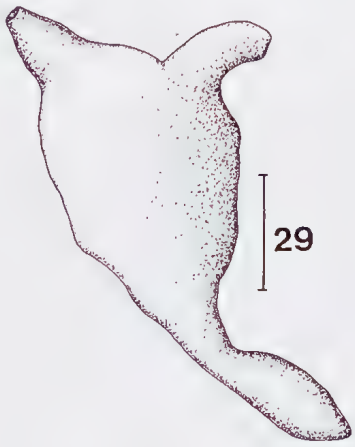
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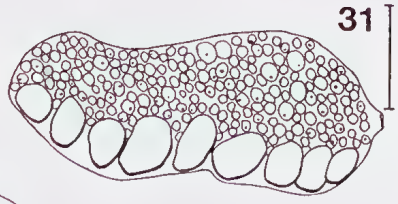
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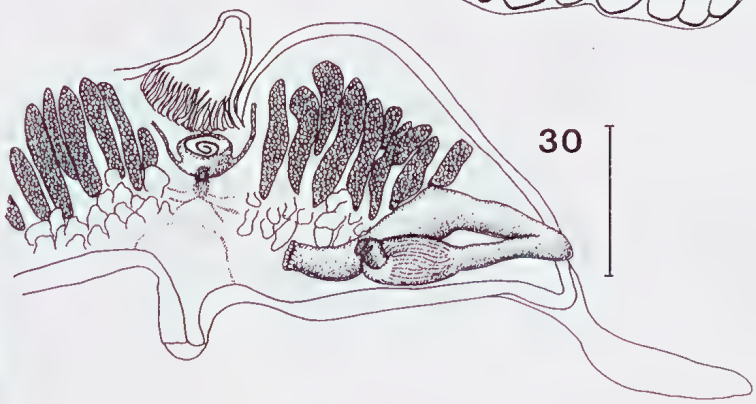
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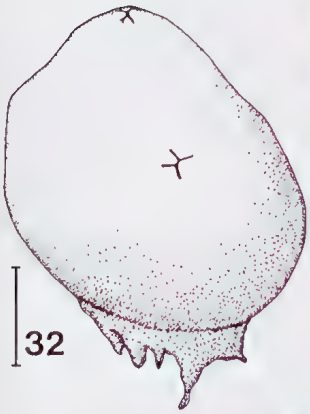
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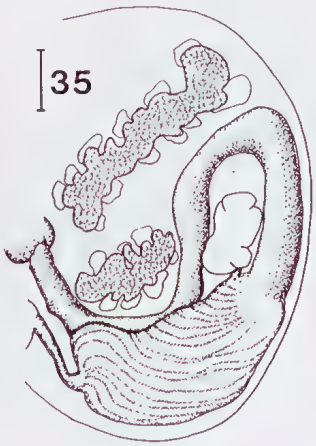
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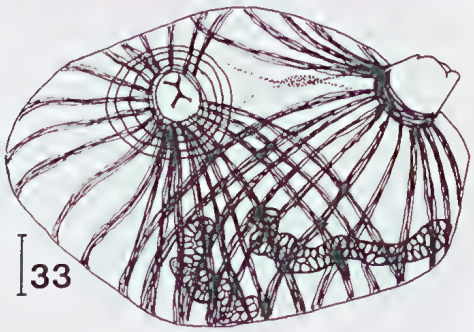
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extends across the body wall anterior to the pole of the gut loop. Endocarps are scattered on the body wall between the gonads.

REMARKS

Cnemidocarpa tripartita Kott, 1985 from Bass Strait has, like the present species, a rounded body, white (but thin) translucent test, 3 branchial folds on each side of the body, a long stomach with longitudinal folds, an endocarp enclosed in the pole of the gut loop, and 2 gonads on the left and 3 on the right. Its significant differences from the present species are its low branchial folds with only 2 or 3 internal longitudinal vessels (while those of the present species are broad and flat with 12 or 13 longitudinal vessels), its light attachment of the gonads to the body wall by fine ligaments (while in the present species gonads are embedded) and the absence of endocarps on the body wall between the gonads.

Genus **Asterocarpa** Brewin, 1946

Asterocarpa humilis (Heller, 1878)

Styela humilis Heller, 1878, p.26.
Asterocarpa humilis: Kott, 1985, p.141 and synonymy.
Not *Cnemidocarpa* aff. *humilis*: Monniot, 1991b, p.25.

DISTRIBUTION

RECORDED RANGE: This species is known from temperate waters from Albany, across the southern coast of Australia to Tasmania and Victoria, New Zealand, and from South Africa and the eastern Pacific (see Kott 1985).

REMARKS

The specimen from tropical New Caledonian waters which Monniot (1991b) believed to have affinities with this species has 2 long, branched gonads across each side of the body, between the ventral and dorsal mid-line, converging to the atrial aperture. The short, cnemidocarp-type gonoducts are at the dorsal (distal) end of each gonad. This contrasts with the genus *Asterocarpa* which has irregularly branched gonads, with ventrally directed gonoducal openings, around the ventral margin of the right side of the body, and one in a similar (ventral) position anterior to the gut loop on the left. The New Caledonian specimen also has more longitudinal branchial vessels than the temperate species *Asterocarpa humilis*.

Cnemidocarpa lobata Kott, 1985 has undulating branched gonads, like the New Caledonian specimen, but it has a particularly long gut loop and also is temperate. The New Caledonian specimen appears either a small (1cm diameter) specimen of *Cnemidocarpa stolonifera*, or the related *C. pedata* which has a short stomach like Monniot's specimen.

Genus **Polycarpa** Heller, 1877

Polycarpa aurita (Sluiter, 1890)

Styela aurita Sluiter, 1890, p.338.
Polycarpa aurita: Kott, 1985, p.152 and synonymy. Monniot, 1987b, p.294. Nishikawa, 1991, p.92.
Polycarpa insulsa: Monniot 1987b, p.294 and synonymy.

DISTRIBUTION

RECORDED RANGE: The species apparently is pantropical, being recorded from the Caribbean, as well as from the Japan Sea, Indonesia, New Caledonia and the Philippines, north-western and north-eastern Australia, and south to Cockburn Sound and Port Jackson respectively.

REMARKS

Van der Sloot (1969) believed there to be 2 species, a Caribbean one, consisting of *P. insulsa* (Sluiter, 1898) and its synonyms, and a western Pacific one, *P. circumarata* (Sluiter, 1904) which Kott (1985) and Monniot (1987b) believe to be a junior synonym of *P. aurita* (Sluiter, 1890). The distinctions between the Atlantic and Pacific species which were established by Van der Sloot are differences between the type specimen of *P. circumarata* (lacking gonads in the posterior end of the body) and the Caribbean populations. This distinction can be sustained only if specimens from the Western Pacific never have gonads on the posterior part of the body wall. In fact, specimens from Australian waters show a great range in the distribution of gonads. Other distinctions such as the tough lining of the atrial cavity, which is said to occur in *P. insulsa*, occur also in *P. aurita*.

A problem with the separation of the Pacific and Atlantic species, is that specimens of the former have a range in characters, such as the number of internal longitudinal vessels, the consistency of the test and surface projections from it, that transcends any of the currently recognised differences between the species. Thus, although it is always difficult to justify genetic continuity

for pan-tropical species, the present evidence supports such a range for this species.

The occurrence of the specimen from New Caledonia assigned to *P. insulsa*: Monniot, 1987b, which is said to be identical with specimens from the Caribbean, adds support to the view that there is no distinction between these species.

Polycarpa contecta (Sluiter, 1904)

Styela contecta Sluiter, 1904, p.66. Kott, 1985, p.162.
?C. Monniot, 1987b, p.291.

DISTRIBUTION
RECORDED RANGE: The species is recorded from Indonesia, and Townsville, and possibly from New Caledonia.

REMARKS
Monniot (1987b) remarks that his (single) specimen from New Caledonia corresponds well with Kott's (1985) description (based on the Siboga type material and specimens from Townsville). However, it does differ in 3 important respects. The opening of the neural gland is not the deep S-shaped slit — which Kott (1985) believes to be characteristic of *P. contecta*, its gonads are embedded in thick endocarp while those Kott examined are attached by a membrane along the proximal half of each, and the stomach of *P. contecta* is characteristically long, occupying most of the proximal limb of the primary gut loop while that of the New Caledonian specimen is shorter. Thus, there is some doubt about the assignation of the New Caledonian specimen.

Genus **Polyandrocarpa** Michaelsen, 1904

Polyandrocarpa colemani n.sp.
(Figs. 36–41, 44)

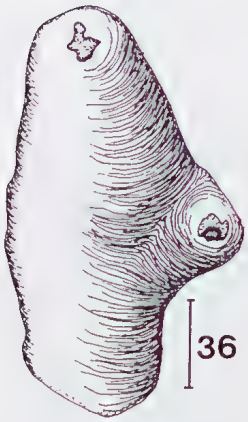
DISTRIBUTION
TYPE LOCALITY: New South Wales, off Queensland border (Cook I., 9m, north side of I. rocky bottom, coll. N. Coleman January 1987, holotype QM GH5724; Arrawarra, 12m, south face of North Rock, coll. AIMS Bioactivity Group 19.2.88, paratype, QM GH5392).
FURTHER RECORDS: New South Wales (Coffs Harbour, photographed specimens; Cook I., QM GH5725).
The species grows along the top of of ridges where it is subjected to maximum current flow.

DESCRIPTION
EXTERNAL APPEARANCE: Colonies are firm, massive, to 1m long and about 0.3m wide, opaque and grey, with white rings around the apertures. The apertures protrude from the otherwise smooth surface of the colony on short cylindrical siphons. Branchial apertures are bent over to lie on the surface while the atrial apertures are directed upwards. The apertures appear to have smooth rims, the usual 4 lobes usually characteristic of styelid ascidians not being evident. In preservative the external test is dark grey, but internally the test is whitish, translucent and gelatinous, without embedded nor encrusting sand. The dark zooids are completely embedded in the tough test, and are evenly spaced. They protrude only slightly from the surface of the colony. They lie on their ventral surface with the dorsal surface uppermost, near the outer surface of the colony. Blood vessels anastomose through the thick gelatinous internal test.

INTERNAL STRUCTURE: Zooids are muscular, and much contracted in the available colonies. From the base of the branchial siphon to the posterior end of the contracted body is about 1cm. The siphons are sometimes long and thin, but in other specimens they are withdrawn and the apertures appear sessile. Externally circular muscles form an almost complete layer. The internal longitudinal muscles are less crowded. Branchial tentacles are long and pointed, and number about 50. The peritubercular area is a shallow V. The opening of the neural duct is a long, sessile slit, oriented transversely, longitudinally, or obliquely, and affected by the body's contraction — the transverse slit sometimes being bent into a U- or V shape. The slit often is obscured by the closely papillated and wrinkled lining of the prebranchial area, although this also may be caused by contraction of body wall muscles.

The branchial sac is robust, with conspicuous longitudinal vessels arranged according to the following formula: DL0(4)1(6)1(8)1(5)1E. Stigmata are 6 per mesh in the middle of the branchial sac, and 8 per mesh between the first fold and the plain-edged, long, dorsal lamina. The oesophagus is also long, curving up posteriorly toward the oesophageal opening.

The oesophagus is short. The long stomach, occupying about three-quarters of the ascending limb of the gut loop, is narrow at the cardiac end, gradually increasing in width to its junction with the wide intestine. There are 18 internal longitudinal stomach folds. A small, straight caecum is at the distal end of the stomach, in the inside curve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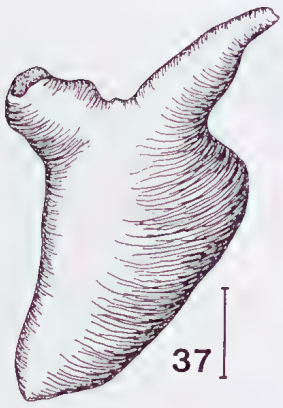
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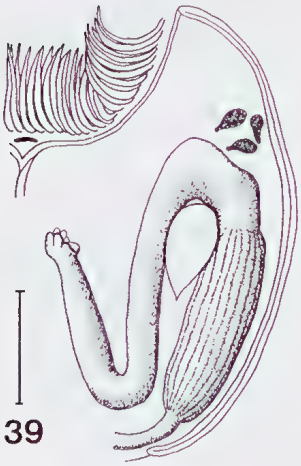
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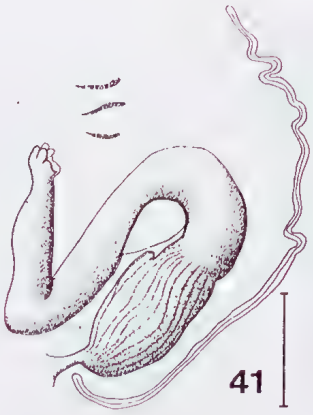
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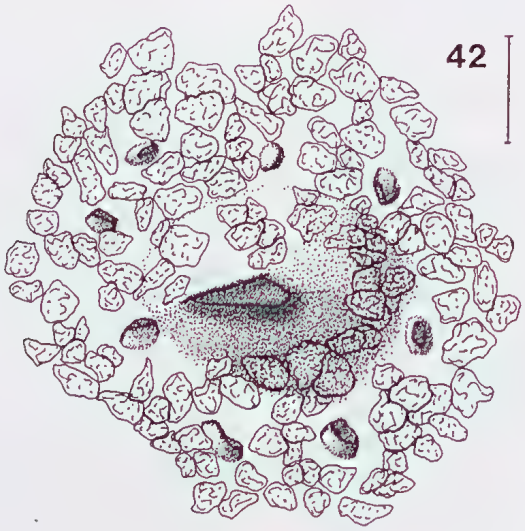
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of the loop, crowded between the stomach and the short, comma-shaped, flat-topped endocarp which is enclosed in the pole of the gut loop. The descending limb of the narrow primary gut loop is parallel to the ascending limb, although this could be an artefact resulting from contraction. The rectum is long. Although there is some variation in its length relative to the descending limb of the primary loop, this variation may also be the result of contraction. The anal border has 4 to 6, sometimes subdivided, deep lobes on its dorsal rim. The opposite side is undivided.

Gonads are present only in the holotype colony. They are long, narrow polycarps lying on, rather than embedded in, the body wall. Immature ova fill the ovarian tube, but male follicles are not developed in any of the zooids examined. On the left are up to 4 gonads in a row in the middle of the body wall, sometimes with an additional one dorsal to them in what may represent an incomplete second row. In one zooid a rather irregular clump of 3 polycarps is near the pole of the gut loop, just to the left of the endostyle. On the right, gonads are seldom present, being observed in only 2 of approximately 10 zooids examined. They are in one or 2 incomplete rows on the dorsal half of the body wall, and are directed toward the atrial aperture. The lining of the parietal wall of the atrial cavity is foamy with crowded vesicles about 0.05mm in diameter.

Remarks

There are several known species of *Polyandrocarpa* with embedded zooids. Of these, *P. abjornseni* Hartmeyer and Michaelsen, 1928 and *P. simulans* Kott, 1972a (respectively from Western Australia and South Australia) have a simlar flat-topped endocarp in the gut loop, and similar numbers of branchial vessels to the present species. However, they both lack the great mass of zooid-free test that is characteristic of the present species. *Polyandrocarpa robusta* Sluiter, 1915 (which Kott, 1985, thought may be similar to *P. colligata* Sluiter, 1913) has one to 3 internal longitudinal vessels in the interspaces while the present species never has more than one; and it has a curved stomach caecum, only 14 stomach folds, a smooth anal border, and gonads in a row each side of the endostyle. *Polyandrocarpa maxima*: Van Name, 1918, 1945 from the Philippines and western (*sic*, eastern, Kott 1985) Atlantic has scattered gonads (which may be in a similar position to the gonads in the present species), and a vestigial gastric caecum. Zooids in Van Name's material, however, are crowded with only thin layers of test between them, longitudinal vessels are more numerous both on the folds and in the interspaces, and although the stomach has a similar number of folds to the present species, it is markedly shorter, and the gonads are only loosely attached to the body wall (possibly tending to be upright: see Kott 1985).

Polyandrocarpa colligata Sluiter, 1913 from the Aru Is has a bulky colony, with protuberant apertures, and it closely resembles that of the present species. Also the zooids are similar with similar slit-like openings of the neural duct, a small stomach caecum, a long stomach with apparently a similar number of folds (see Sluiter 1913, pl.VI, Fig. 14) and long, narrow polycarps. Sluiter's species is distinguished from the present one by the course of the gut, and its position across the posterior end of the zooid (features which Sluiter has emphasised do not necessarily constitute a distinction from *P. robusta* since they are readily affected by contraction). *Polyandrocarpa colligata* is also distinguished by its more numerous longitudinal branchial vessels, both in the interspaces and on the folds, its gonads in a row each side of the endostyle (as in *P. robusta*) and the endocarps on the body wall. Other characters conspicuous in the present species and not observed (but possibly overlooked) in *P. colligata* are the foamy layer of vesicles lining the parietal wall of the atrial cavity, and the lobed anal border.

Nevertheless, *P. colemani* has a limited distribution at the boundary of tropical and temperate zones of the eastern Australian coast. It is well isolated from the tropical *P. colligata*.

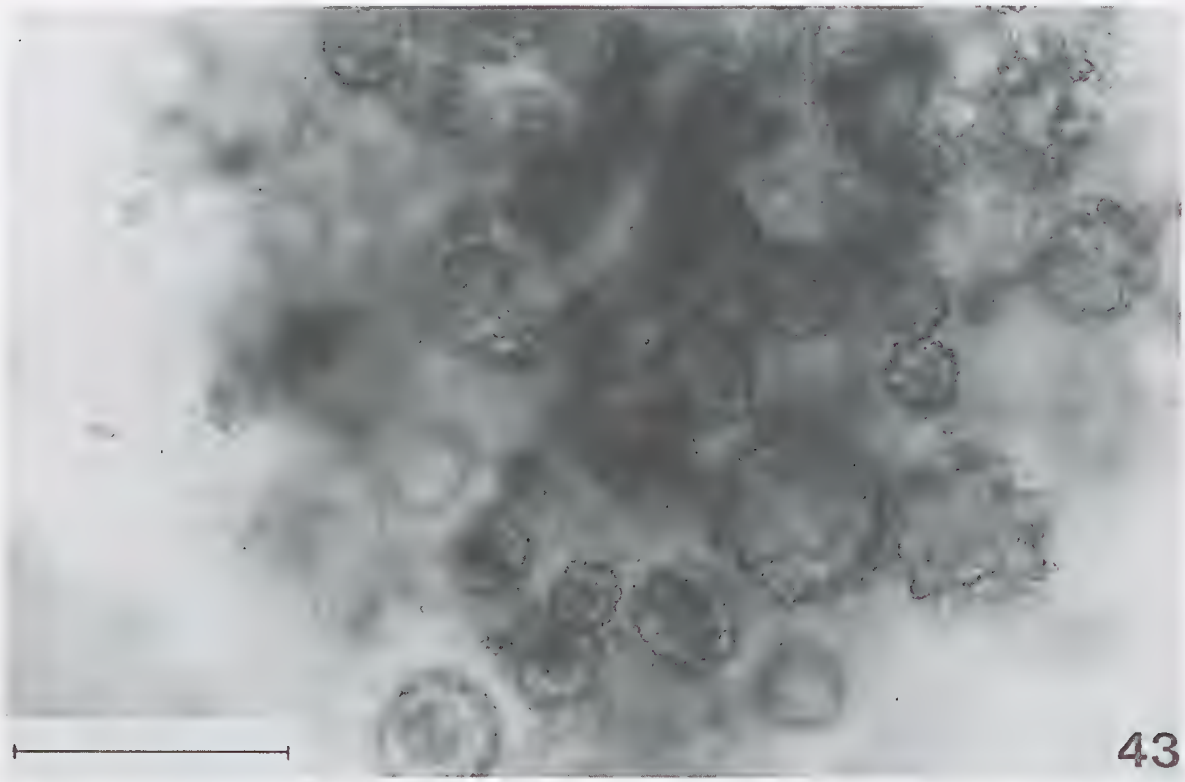
Subfamily BOTRYLLINAE Adams and Adams, 1858

Genus **Botryllus** Gaertner, 1774

Botryllus stewartensis Brewin, 1958 (Fig. 42)

Botryllus stewartensis Brewin, 1958, p.444. Kott, 1985, p.269 and synonymy; 1990b, p.286.

FIGS. 36–42: *Polyandrocarpa colemani* n.sp. (holotype QM GH5724) — 36, 37, bodies removed from test; 38, section across colony showing blood vessels and position of zooids; 39–41, internal organs on left. *Botryllus stewartensis* (QM GH5294) — 42, system showing branchial and common cloacal apertures from above. (Scales: 36, 37, 39–41 — 2mm; 38 — 1cm; 42 — 0.5mm).



FIGS. 43, 44: *Polycitorella coronaria* (QM GH5616) — 43, spicules. 44, *Polyandrocarpa colemani* n.sp. — view of colony (photo, N. Coleman). (Scale: 43, 0.1mm).

DISTRIBUTION

NEW RECORD: Queensland (Point Lookout, QM GH5294).

RECORDED RANGE: The species is known from Albany (WA) across the southern coast of Australian to Port Kembla and Port Stephens (NSW) and Moreton Bay (Qld), as well as Stewart I. and South I. (New Zealand).

Previous records from Moreton Bay are from inside the Bay. The new records are from the ocean side of North Stradbroke I. indicating that Moreton Bay is part of the continuous range of this widespread species, rather than being a refuge at the northern limit of its range.

DESCRIPTION

The colonies are irregular sandy slabs to 5cm or more in maximum dimension, and 1cm thick. They are subdivided into lobes on the surface. About 5 zooids are in each circular system of about 2.0m diameter. Two or 3 systems are crowded into each lobe. Sand particles are embedded in the basal test, and adhere all over the surface. However there is little sand in the tough white internal test, around the zooids.

REMARKS

The present colonies do not have quite such long, narrow stalks as have been previously described. They are otherwise characteristic of this species.

Family PYURIDAE Hartmeyer, 1908
Genus **Pyura** Molina, 1782

Pyura albanyensis Michaelsen, 1927

Pyura albanysensis Michaelsen, 1927, p.193.
Pyura obesa: Kott, 1985, p.315 and synonymy.
Not *Pyura albanyensis*: Monniot, 1989, p.492. Monniot and Monniot, 1991, p.411.

DISTRIBUTION

RECORDED RANGE: The species is known from tropical and temperate waters around the Australian coast, the Arafura Sea, and the Palau Is.

REMARKS

Monniot (1989) distinguishes *Pyura albanyensis* from *P. curvigona* (> *P. vittata*: Monniot, 1989, 1991) only by the presence of the swollen rectum in the latter species. He remarks that 'tous les autres caractères sont peu importants et les différences observées entre les espèces pourraient correspondre à une variabilité'. However, there are significant differences in a number of conspicuous and stable characters between these two species. The principal difference is the form of the siphonal spines (Kott 1985). In *P. curvigona* these have a flat scale halfway along them, which is not present in *P. albanyensis*. In *P. albanyensis* the needle-like spines are of two sizes. Further differences are the short dorsal lamina, the long, deeply curved U-shaped gut loop and the distinct longitudinal stripes down the outside of the siphons in *P. albanyensis*. The species are similar only in the crowded endocarps on gut loop and gonads, in the almost pinnate form of the ovarian tube, each short branch with a cap of male follicles, and in the distribution of the siphonal spines, which continue over the outer surface from inside the siphon.

Monniot (1989) assigned 2 specimens from New Caledonia, one 5cm and one 1.2cm long, to *P. albanyensis*. In neither were the small spines between the larger ones reported, nor can they be detected in Monniot's scanning electron micrographs. It is possible that these have been obscured by the larger spines, although this does not seem to be the case. The smaller spines, like the larger ones, are on the surface of the test both inside and outside the siphons, and should be apparent if they are present.

Further, although the gut loop and gonads have crowded endocarps on them, and the long ovarian tubes have pinnate branches, each with a cap of terminal testis follicles, the New Caledonian specimens differ from *P. albanyensis* in having a long dorsal lamina and a narrow but gently curved gut loop.

The form of the siphonal armature needs to be established by light microscope examination of cleared preparations in order to accurately assign the New Caledonian specimens.

Monniot(1989) drew attention to the fact that the name Hartmeyer applied to the holotype of this species is preoccupied by the Antartic *Pyura obesa* Sluiter, 1912.

Pyura curvigona Tokioka, 1950

Pyura curvigona Tokioka, 1950, p.147. Kott 1985, p.296 and synonymy.
?*Pyura vittata*: Monniot, 1989, p.490.
?*Pyura uatio* Monniot, 1991b, p.33.

DISTRIBUTION

RECORDED RANGE: The species is known from Shark Bay (Western Australia), Heron and Lizard I. (Queensland), the Palau Is, Indonesia (see Kott 1985), and possibly from New Caledonia.

REMARKS

Monniot (1989) has synonymised this species with the Atlantic Ocean *Pyura vittata*. He appears to have overlooked the opalescent scale which is such a feature of the siphonal armature of the present species (see Kott 1985, Figs 5k, 145a,b). Since the New Caledonian specimens assigned to *P. vittata* have the enlarged rectum, pinnate gonads, and endocarps of the present species it is possible that they are conspecific. Examination of cleared preparations of siphonal armature by light, rather than by scanning electron, microscopy, would, if they are present, display the scales of the siphonal spines which are just under the surface of the test.

The green liver and pink body wall of this species is found also in *P. uatio* from New Caledonia which, however, lacks an expanded rectum, and may be a different species.

Pyura rapaformis Kott, 1990
(Figs 45, 46)

Pyura rapaformis Kott, 1990b, p.287.

DISTRIBUTION

NEW RECORD: South Australia (Beachport Jetty piles, SAM E2510).

RECORDED RANGE: The species, previously recorded from the upper surface of a reef at Cottesloe, probably has a continuous range between Cockburn Sound and St Vincent Gulf.

DESCRIPTION

The present specimens are as previously described, with both apertures on the upper, more or less flattened, surface of a turnip-shaped body. The surface test has irregular extensions and papillae to which sand adheres, and sand also is embedded in the test. The body has a posterior stolon projecting down into the test. The siphonal spines are about 0.08mm long, with a long narrow opening and 4 rounded knobs at the posterior end of the shaft. Branchial tentacles are feathery, with long primary branches. The branchial sac has 6 wide, overlapping folds on each side with 7 to 18 internal longitudinal vessels on the folds and up to 3 between. Leafy, irregular endocarps are on the gut and gonads.

REMARKS

Externally the species resembles individuals of *Pyura isobella* Kott, 1985 from Ulladulla (NSW) and internally it has similar endocarps and gut loop and gonads. The siphonal spines lack the posterior expansion, and the small opening of spines of *P. isobella*, and more closely resemble the spines of *P. tasmanensis* Kott, 1985 (as observed by Kott 1990b).

Genus **Herdmania** Lahille, 1888

Herdmania momus (Savigny, 1816)

Cynthia momus Savigny, 1816, p.143.
Herdmania momus: Kott, 1985, p.338.
Pyura momus: Monniot, 1989, p.498.

DISTRIBUTION

RECORDED RANGE: The species is pantropical, extending into temperate waters of southern Africa and southern Australia.

REMARKS

Monniot (1989) believes the genus *Herdmania* to be a junior synonym of *Pyura*. In addition to the characteristic long barbed spines, *Herdmania* has a continuous ovarian tube surrounded by male follicles, rather than being broken up into separate gonad blocks as in *Pyura*; and the liver lobules are embedded in the body wall, rather than lying free in the atrial cavity as in *Pyura* (see Kott 1985).

Genus **Microcosmus** Heller, 1877

Microcosmus tuberculatus Kott, 1985

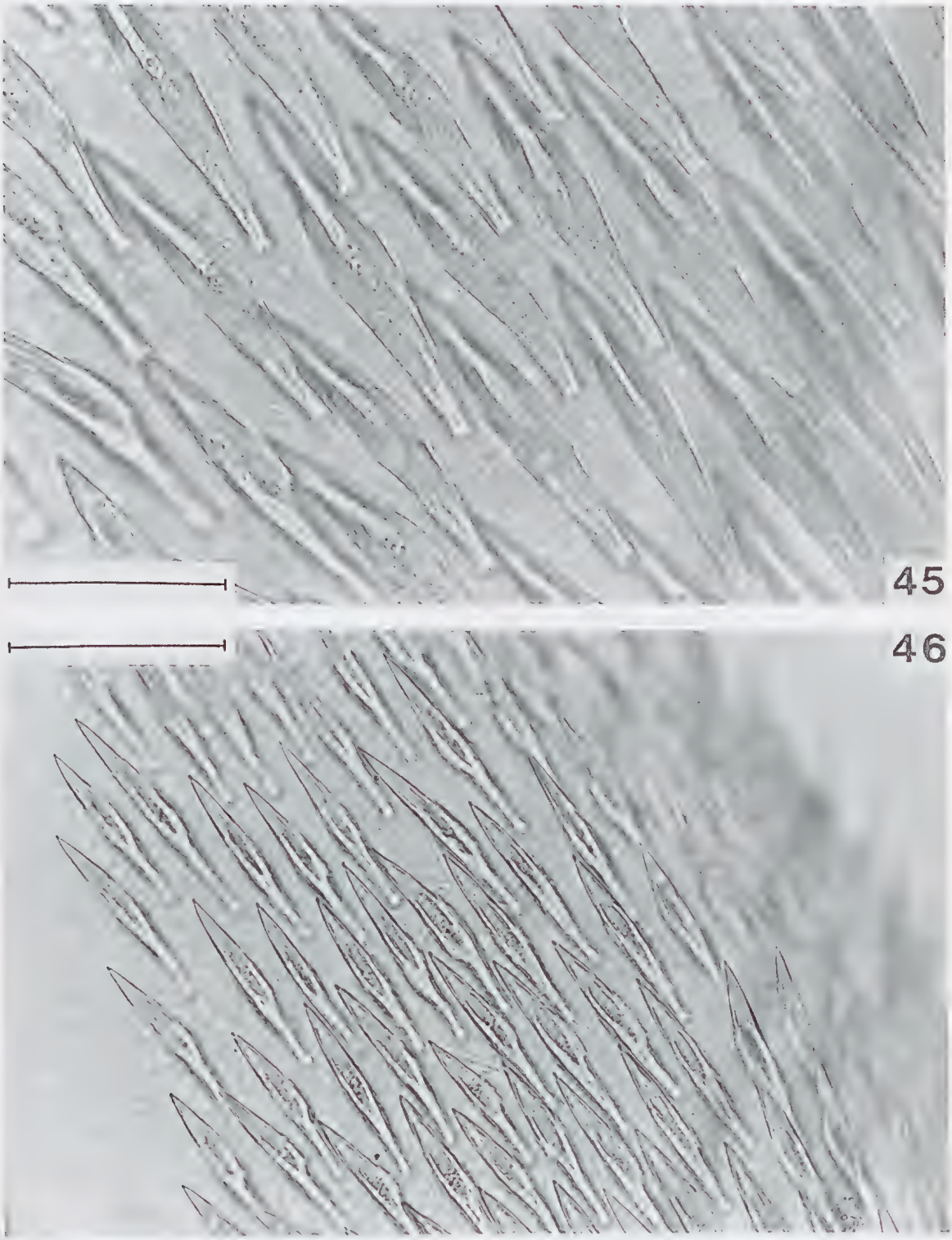
Microcosmus tuberculatus Kott, 1985, p.361. ? Monniot, 1991b, p.31.

DISTRIBUTION

RECORDED RANGE: The species is known for certain only from its type locality in the Swain Reefs.

REMARKS

The species is distinguished from *M. exasperatus* by its large conspicuous conical spines around and lining the apertures (see Kott 1985, Fig. 179b) and the deeply incised anal border. The specimen from New Caledonia (Monniot 1991) has neither of these features. The thick endocarp-like layer of the body wall Monniot observed over the gonads and gut occurs variably in most *Microcosmus* species, including *M. exasperatus*, to which the New Caledonian specimens very likely belong.



FIGS. 45, 46: *Pyura rapaformis* (SAM E2510) — siphonal spines (Scales: 45, 0.05mm; 46, 0.1mm).

Family HEXACROBYLIDAE Seeliger, 1906

The family was reviewed by Kott (1989a), and later, by Monniot and Monniot (1990).

The family is characterised by its large buccal cavity, surrounded by 6, usually large, branched branchial arms, a large kidney, and a reduced perforated pharynx, limited to a short band at the proximal end of the gut. Ciliated stigmata are small and rounded. The gut is well developed with a wide, and often long oesophagus, and there is evidence of adaptation for a carnivorous habit (see Kott 1989a). Although, successively, a new pleurogonid suborder, Aspiraculata Seeliger, 1906, and a new tunicate class Sorberacea Monniot, Monniot and Gaill, 1975 have been proposed for the family, there appears to be no justification for either of these higher taxa (see Kott 1989a).

The Hexacrobylidae have adaptations for deep water habitats, but their morphology is homologous with that of Molgulidae, with which they appear to have closer affinities than the latter family has with other extant ascidian taxa, even within the Pleurogona (see Kott 1989a).

The view (Monniot and Monniot 1990) that the family name Hexacrobylidae should be abandoned in favour of Oligotrematidae (sic. Oligotremidae Monniot and Monniot, 1990) is incorrect (ICZN Article 40). Further, the type genus is *Hexacrobylus* Sluiter, 1905a, a junior objective synonym of *Oligotrema* Bourne, 1903.

Although Kott (1985) thought the family was not represented in Australian waters, *Asajirus indicus* Oka, 1913 and *Oligotrema psammites* Bourne, 1903 have since been recorded (Kott 1989a).

Genus **Asajirus** Kott, 1989a

Type species: *Hexacrobylus indicus* Oka, 1913.

Kott (1989a) examined and redescribed the type specimen (ZMA TU564) of *Hexacrobylus psammatodes* Sluiter, 1905a, and found it to be a species of the genus *Oligotrema* Bourne 1903, possibly conspecific with its type species *O. psammites* Bourne, 1903 from New Britain. Thus was corrected a belief that *Hexacrobylus psammatodes* and *H. indicus* Oka, 1913 were congeneric, and *H. indicus* Oka was found to be a member of an undescribed genus. *Hexacrobylus indicus* Oka, 1913 was therefore designated type species of a new genus *Asajirus* Kott, 1989a (of which *Hexadactylus* Monniot and Monniot, 1990, with the same type species as *Asajirus*, is a junior synonym).

Monniot and Monniot (1990) recognise 12 species in the genus *Asajirus*, distinguished from one another primarily by differences in the length of the vas deferens and in the number and length of testis lobes. It may be difficult to sustain this number of species, in view of the probability that there is some intraspecific variation in taxa which, in many cases, have vast geographic ranges.

The differences are less compelling than the similarities between most of the species Monniot and Monniot (1990) have documented, and many are sympatric in at least part of their range, while some are over their whole range. For instance, *A. longitestis* (Monniot and Monniot, 1990), *A. ovirarus* (Monniot and Monniot, 1990), *A. hemisphericus* (Monniot and Monniot, 1990), *A. gulosus* (Monniot and Monniot, 1984b) and *A. indicus* (Oka, 1913) are all recorded from the vicinity of New Caledonia, *Asajirus millari* (Monniot and Monniot, 1991) also is from the West Pacific (the Bali Sea); *A. seeligeri* (Monniot and Monniot, 1990) and *A. gulosus* are from the Comoro Is in the Indian Ocean and some records of *A. indicus* are also from the Indian Ocean; *A. ledanoisi* and *A. eunuchus* are from wide ranges in the Atlantic, and *A. arcticus* is from the Norwegian Sea; while *A. antarcticus* is recorded from around the Southern Ocean and *A. dichotomus* is from the southeastern Atlantic (the Cape Basin).

It is not intended to review this genus in the present work, rather attention is drawn to some of the problems of species definition in this family. These will not be resolved if descriptions do not take account of the homologies of organs, of similarities in morphology as well as morphological differences, of probable artefacts resulting from contraction and distortion, and of differences that most likely arise from growth and maturity.

Asajirus indicus (Oka, 1913)

Hexacrobylus indicus Oka, 1913, p.6. Millar, 1959, p.203; 1969, p.97; 1970, p.146; 1975, p.332. Monniot and Monniot, 1968, p.32; 1970, p.334; 1979, p.564; 1984b, pp.198 (figs 1,2) 203; 1987, p.41. Monniot, F., 1971, p.458.

Asajirus indicus: Kott, 1989a, p.521.

Hexadactylus indicus: Monniot and Monniot, 1990, p.271.

Hexacrobylus arcticus Hartmeyer, 1923, p.133. Monniot and Monniot, 1984b, p.203 (specimens from *Norbi* cruise).
Hexadactylus arcticus: Monniot and Monniot, 1990, p.261.
Hexacrobylus eunuchus Monniot and Monniot, 1976, p.658.
Hexadactylus eunuchus: Monniot and Monniot, 1990, p.265.
Hexacrobylus sp. Monniot and Monniot, 1982, p.128 (part, Eltanin cruise 5, station 258).
Oligotrema psammites: Kott, 1969, p.168.
Hexadactylus antarcticus Monniot and Monniot, 1990, p.259.
Hexadactylus longitestis Monniot and Monniot, 1990, p.275.
Hexadactylus millari Monniot and Moniot, 1991, p.277.
Hexadactylus seeligeri Monniot and Monniot, 1990, p.281.

DISTRIBUTION

NEW RECORDS: Coral Sea (12° 05' S 146° 24'E, *Cidaris* 3 site 6.1, 16.2.92, 3319–3105m, QM G300891; 13° 29'S 147° 13'E *Cidaris* 2 Site 15.1, 5.9.88, 2542–2457, QM G300892.

RECORDED RANGE: The recorded range for *A. indicus* and its probable synonyms is: *A. longitestis* — New Caledonian (both sides of the Norfolk Ridge); *A. indicus* — the Indian Ocean, New Caledonia, off eastern Australia from 151°27' to 148°38'E and 12° to 42°S from the Coral Sea to eastern Tasmania; *A. seeligeri* — the Indian Ocean and Comoro Is.; *A. millari* — the Bali Sea (western Pacific); *A. eunuchus* — southwestern and northern Atlantic; *A. arcticus* — northeastern Atlantic; *A. antarcticus* — South Indian and Pacific Oceans.

The species is found at depths from 1000 to 5000m. The record for the specimen AM Y2125 from off the New South Wales coast, is from 151°27'E, not 51°27'E as reported by Kott (1989a).

DESCRIPTION

The newly recorded specimens are rounded posteriorly, 1.2 cm long, but contracted anteriorly, causing the fine hairlike projections mixed with foraminifers and other paricles to appear more crowded than they are posteriorly. Internally the 2 ventral muscle bands are short and broad. the rectum is crowded with hard particles including foraminifers, polychaetes, ostracods, cladocerans, isopods, gastropods and what appears to be particles of ophiurid (including spines). The remainder of the gut (the long oesophagus and stomach) are empty.

REMARKS

Specimens from the northern Atlantic (*A. ledanoisi*) and from the Cape Basin, south-eastern Atlantic (*A. dichotomus*) with long sperm ducts are not included in the above synonymy of *A. indicus*, although *A. eunuchus* (Monniot and Monniot, 1976) from the south-western and northern Atlantic, *A. arcticus* (Hartmeyer, 1923) from the Norwegian Sea, *A. antarcticus* (Monniot and Monniot, 1982) from the southern (polar) Indian and Pacific Oceans and *A. millari* from the Bali Sea have short male ducts as in *A. indicus*, and are here included in its synonymy, as is *A. seeligeri* (with both short on long male follicles) from the Indian Ocean, and *A. longitestis* (with long male follicles) from New Caledonia. *Asajirus indicus* (Oka, 1913) as well as being taken from off the eastern Australian coast, is from the Indian Ocean and New Caledonia.

Also from New Caledonia, and, for the present, excluded from the synonymy of *A. indicus*, are *Asajirus hemisphericus* and *A. ovirarus*, with more or less entire testis; and *A. gulosus* with a long vas deferens like *A. ledanoisi* and *A. dichotomus*.

Genus **Oligotrema** Bourne, 1903

Type species: *Oligotrema psammites* Bourne, 1903.

Although not designated a neotype, Monniot and Monniot (1990) redescribed the species from a specimen taken from near the type locality.

Monniot and Monniot's definition of the genus omits certain significant characteristics described by Bourne, which also are present in the type specimen of *Hexacrobylus psammatodes* Sluiter, 1905a (see Kott 1989a). Monniot and Monniot (1990) refer to the widely separated apertures but not to the posterior position and orientation of the atrial aperture; they refer to muscles extending the length of the body wall, but fail to indicate that these are circular muscles, sometimes interrupted; and that longitudinal muscles are very limited; nor do they refer to the flagellated epithelial covering of the branchial tentacles described by Bourne (see also Kott 1989a).

Monniot and Monniot (1990) indicate, as Kott (1989a) had suggested, that the branchial stigmata are circular perforations, rather than the rectangular stigmata described by Bourne. This removes the principal restraint to the synonymy of *H. psammatodes* Sluiter, 1905a with the present species. Other characters, viz. the branchial

tentacles, the large endocarps and the large atrial cavity, are as described by Bourne, and by Kott (1989a) for the type specimen of *H. psammatodes* Sluiter, 1905a (ZMA TU564).

There is no additional evidence regarding the proposed synonymy of *Gasterascidia*, *Sorbera* with *Oligotrema* (see Kott 1989a). Nor is there any clarification regarding the apparent degeneration of the rectum in *Gasterascidia lyra*, which, if present, appears to be non-functional (see Monniot and Monniot, 1990 Fig. 5B).

Oligotrema psammites Bourne, 1903

Oligotrema psammites Bourne, 1903, p.233. Monniot and Monniot, 1990, p.253.

Hexacrobylus psammatodes Sluiter, 1905a, p.135; 1905b, p.135.

Hexacrobylidae juv., intermediate between *Sorbera* and *Gasterascidia*: Monniot and Monniot, 1984b, p.212; 1990, p.257.

?*Sorbera digonas* Monniot and Monniot, 1984b, p.209.

Oligotrema psammatodes: Kott, 1989a, p.529. Monniot and Monniot, 1990, p.258.

DISTRIBUTION

RECORDED RANGE: The species is recorded from New Britain (Bourne 1903; Monniot and Monniot 1990), Indonesia (ZMA TU564, Siboga, Station 211, Banda Sea, Sluiter 1905a), west of New Caledonia (Monniot and Monniot 1990); New South Wales coast (Kott 1989a) and the south-east Atlantic (the Cape Basin, Monniot and Monniot 1984b).

Sorbera digonas is recorded from the tropical Indian Ocean.

REMARKS

The specimens all have the shallow ventral groove in the pharynx; vertically flattened branchial tentacles with one or 2 short, pointed, projections anteriorly, an otolith-like black granule in the neural gland, and the parietal wall of the atrial cavity raised into long endocarps on each side of the oesophagus. These endocarps sometimes cover part of the gonads. In the thick pharyngeal wall the interconnected chambers (that the Monniots in 1984 and 1990 refer to as branching tubules) eventually open to the atrial cavity by small, rounded ciliated stigmata which vary in number according to the size of the specimen. The ligament attaching the oesophagus to the body wall (Kott 1989a) appears to be the ventral septum dividing the atrial cavity into two sections (Monniot and Monniot 1990). In fact, the atrial invagination is always from the dorsal surface and the cavity always is continuous over the dorsum. It never penetrates ventral to the pharynx, past the ventral sinus. The ligament or septum is merely the ventral body wall where it is not interrupted by the atrium.

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TWO NEW GENERA OF MARINE ISOPOD CRUSTACEANS (CIROLANIDAE) FROM MADANG, PAPUA NEW GUINEA

NIEL L. BRUCE

Bruce, N.L. 1993 06 30: Two new genera of marine isopod crustaceans (Cirolanidae) from Madang, Papua New Guinea. *Memoirs of the Queensland Museum* **31**(1): 1-15. Brisbane. ISSN 0079-8835.

Aatolana gen.nov. is characterized by lobate pleopod peduncles, medially indented cephalon anterior margin, and posteriorly acute epimera on pleonite 3. *Aatolana rapax* sp.nov., the type species, is described from specimens trapped at depths from 150-450m off the outer reef slope at Madang. *Aatolana schiodtei* comb.nov. is transferred from the genus *Cirolana*. *Plakolana* gen.nov. is characterised by flattened posterior pereopods provided with long setae and spines, a medially indented cephalon anterior margin, elongate frontal lamina, quadrate pleopod 1 peduncle and the unique shape of the epimera of pleonite 3. *Plakolana accola* sp.nov., the type species, is described from trapped specimens off the outer reef slope at Madang, at depths from 300 to 450m. *Plakolana nagada* sp.nov. occurs within the barrier reef in shallow (16-22m) silty or sandy bottoms. *Plakolana* sp. and *P. binyana* comb.nov. are transferred from *Cirolana*. Both genera are known only from the Southwest Pacific. □*Isopoda, Cirolanidae, new genera, new species, Aatolana, Plakolana, southwest Pacific, taxonomy.*

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Published reports devoted to the marine isopod fauna of New Guinea are few (see Bruce, 1982, Jones et al., 1983) although a number of records have recently been published as part of longer reports (e.g. Bruce, 1986a,b; Bruce & Harrison-Nelson, 1988; Williams & Williams, 1992). The nearby region of tropical and subtropical Queensland has receeived more attention from isopod taxonomists, and there the family Cirolanidae is represented by 52 species in 12 genera (although numerous species still remain to be described).

In 1989, I spent three weeks at the Christensen Research Institute at Jais Aben, Madang surveying the isopod fauna of the reefs and, to a lesser extent, near-reef sediments, from the intertidal to a depth of about 30m. Cirolanids were sampled at greater depths by the use of baited traps. The area proved to have a rich and diverse isopod fauna with well in excess of 100 species. With more thorough sampling of particulate sedimentary habitats this total should rise even further.

The family Cirolanidae is represented in the Madang collection by about 27 species in 11 genera, indicating a very high diversity when compared to figures available for single localities elsewhere. For example, Heron Island, a well collected location at the southern end of the Great Barrier Reef has 16 species in 7 genera (Bruce, 1986a). The entire Caribbean region has a total 22 free-living species (Kensley & Schotte, 1989), while Aldabra Island, in the Western Indian Ocean, when surveyed by Kensley (1988), yielded only 3 species.

MATERIAL AND METHODS

Specimens were collected using methods described in Bruce (1986). Appendages were dissected from the right side of the specimen unless stated otherwise in the figure captions. All species described here were collected by setting baited traps overnight. The trap design is a 'minnow trap' made of storm drain piping fitted with end caps to which cut off funnels had been fitted.

Drawings of appendages were made using a compound microscope for *Plakolana* and a dissecting microscope for the larger *Aatolana*.

Pereopod orientation is identified as anterior (= superior) and posterior (= inferior); the margin to which the dactylus folds is regarded as posterior in both pereopods 1-3 and 4-7, even though the orientation of the posterior limbs is reversed; the lateral surface is the outward facing surface of the pereopod, and mesial is inward facing. Anterior (An) and posterior (Po) are identified on Fig 2.

Specimens have been deposited at the Queensland Museum (QM), Australian Museum (AM) and Museum of Victoria (NMV). Voucher samples have been donated to the San Diego Natural

History Museum. PMS= plumose marginal setae; BL= body length.

TAXONOMY

General Remarks

Bruce (1986a: 223) listed a number of cirolanid species as incertae sedis, all but one being retained in *Cirolana*. Since that time only one, *Protognathia bathypelagica* (Schultz, 1977) has been relocated (Wägele & Brandt, 1988). Two of the species described by Bruce (1986a), *Cirolana schiodtei* Miers and *Cirolana* sp., were regarded as not conforming to the concept and diagnosis of *Cirolana*, but establishment of new monotypic genera was regarded as premature. Bruce (1991) later described a species that was obviously very similar to *Cirolana* sp. of Bruce (1986a) with the same set of characters that precluded assignment to *Cirolana*. That species was placed in *Cirolana*, also with the caveat of incerta sedis. The discovery of the species described here now provides a solid foundation to establish new genera for these species. In so doing, the generic concept of *Cirolana* can also be refined. It can now be stated that in *Cirolana* (sensu stricto) the anterior margin of the cephalon is with a rostral point or smoothly rounded (never medially indented); pleonite 3 does not encompass pleonites 4 and 5, though pleonite 3 is often posteriorly produced; pleonite 3 (in all Australian species) is narrowly rounded or acute; pereopods 5-7 are without long setae or long spines, and are robust (i.e. have few short spines, and no flattened articles).

Aatolana gen.nov.

Body without tubercles or dorsal sculpture. Cephalon without rostral point, anterior margin medially indented. Eyes large, about 3 times as long as wide. Pereonite 1 about twice as long as pereonite 2. Pleon with 5 visible segments; pleonite 3 with epimera expanded, posteriorly acute, extending to or beyond pleonite 5. Pleotelson with stout spines and PMS.

Antennule peduncle articles of about equal length; article 2 shortest. Antennal peduncle with articles 1-3 short, 4 and 5 longest. Frontal lamina slightly longer than wide; anterior margin curved, visible in dorsal view, with dorsally deflected apical point. Mandible with spine row and molar process well developed; lacinia mobilis absent; incisors assymetrical, right with 3 prominent cusps, left with middle cusp reduced. Maxillule with stout spines on lateral lobe; 3 robust circumplumose spines on medial lobe. Maxilla with all lobes well developed. Maxilliped palp with lateral and medial margin setose; endite with 2 coupling hooks.

Pereopods 1-3 with anterodistal margins of ischium and carpus not produced; posterior margin without elongate spines. Pereopods 5-7 subsimilar. Pereopod 7 with all articles robust, not flattened or natatory; basis with row of setae on posterior margin and lateral carina. Pereopod dactylus without distinct secondary unguis. Penes present on sternite 7, flattened, rectilinear, about twice as long as wide.

Pleopod 1 exopod lateral margin convex, apex narrow. Pleopods 1-3 with both rami with PMS; pleopods 3 and 4 endopods with reduced PMS; endopod of pleopod 5 without PMS. Peduncles of pleopods 1-5 with lateral margin forming, complex refolded lobe. Pleopod 2 appendix masculina basally attached, elongate, longer than endopod. Pleopod 1-4 exopods with slender accessory lamella at posterior proximolateral angle. Uropods with stout spines; mediodistal angle of peduncle produced.

Female: Maxilliped with lamina vibrans in ovigerous specimens. Brood pouch composed of oostegites arising from coxae 1-5. Pleopods 2-5 with accessory lamellae more prominent than in male.

Type Species

Aatolana rapax sp.nov., here designated.

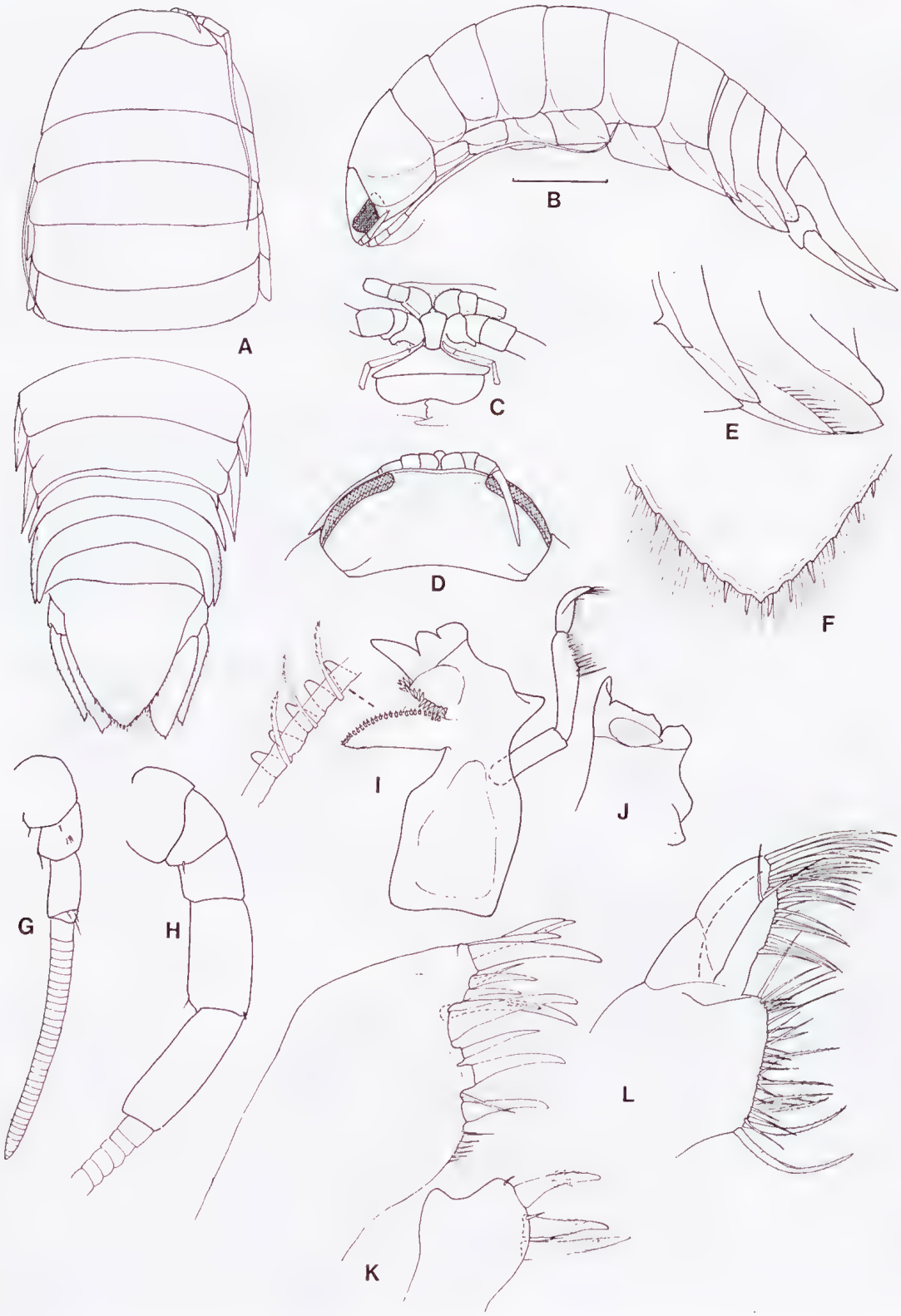
Etymology

From the Greek *Aatos* (insatiable, referring to the ability of this species to devour fish carcasses) combined with *-lana*. Gender is feminine.

Remarks

Characters by which this genus can be identified are the unique apomorphies of the pleopod peduncle lobes and the frontal lamina structure, and also the prominent and posteriorly acute epimera on pleonite 3. Other characters which also identify the genus, though not unique, are the medially indented anterior margin of the cephalon, the shape of pleopod 1 exopod, and the prominent flattened penes. The medially indented anterior margin of the cephalon is a subtle char-

FIG. 1. *Aatolana rapax* sp.nov. A-F holotype, remainder ♂ paratype 32.3mm. A, dorsal view; B, lateral view; C, frons; D, cephalon, dorsal view; E, pleonites, lateral view; F, telson apex; G, antennule; H, antenna peduncle; I, right mandible; J, left mandible incisor; K, maxillule; L, maxilla. Scale represents 4.0mm.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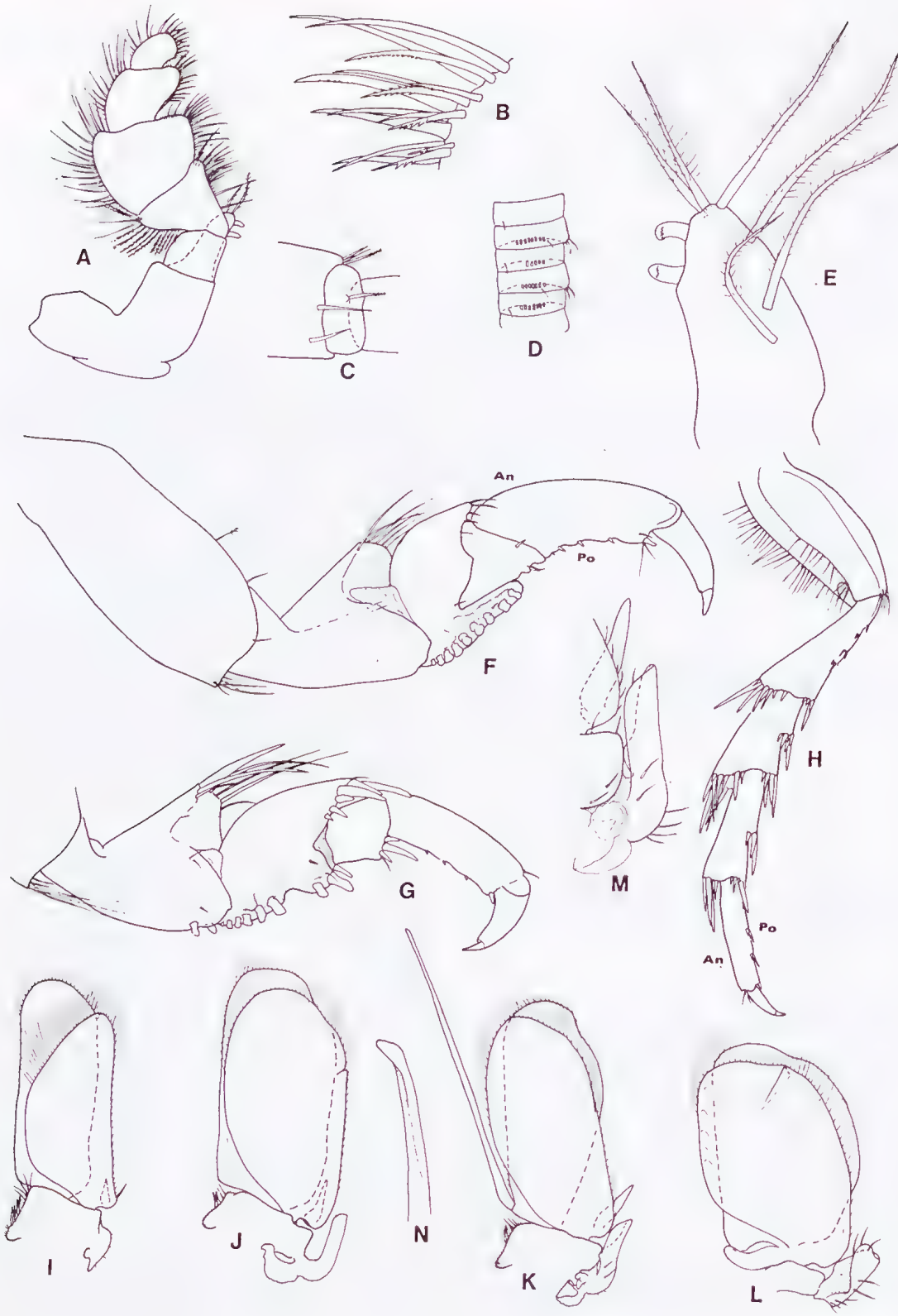
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acter, but is none the less clearly expressed by those genera that show it.

The genus *Cirolana* has no species with medially indented cephalon, flattened rectilinear penes, lobate pleopod peduncles or large epimera on pleonite 3. Additionally *Cirolana* species all have a prominent secondary unguis on the pereopod dactylus and more plumose marginal setae on the endopods of pleopods 3 and 4.

Other Species

Aatolana schioedtei (Miers, 1884) comb.nov. Tropical Australia, from Rottnest Island, Western Australia to Hayman Island (Bruce, 1986a).

Affinities

Aatolana is similar only to *Booralana* Bruce, 1986. Both genera share similar- shaped pleopod rami, have similar elongate eyes, prominent flattened penes, medially indented cephalon and prominent epimera on pleonite 3. The frontal lamina structure of the two genera differ, and in *Booralana* pleonite 2 has well developed epimera, pleonites 2 and 3 both having a ventral flange. Additionally in *Booralana* the pleotelson and uropods are without spines.

KEY TO THE SPECIES OF *AATOLANA*

1. Pleonite 4 posterolateral margin rounded; uropod endopod lateral margin straight; pleotelson dorsal surface never setose ..... *A. rapax*

   Pleonite 4 posterolateral margin acute; uropod endopod lateral margin sinuate; pleotelson dorsal surface of large males setose ..... *A. schioedtei*

Aatolana rapax sp.nov.
(Figs 1-3)

Material Examined

Holotype: ♂(28.7mm), outer reef slope, 5°8.4'S, 145°49.0'E, 3 May 1989, 200-150m depth, baited trap, coll. N.L. Bruce & M. Jebb (QM W17467).

Paratypes: 9♂♂(20.0-32.2mm, m=28.3), 4 ovig ♀♀(29-33mm, mean 30.5), 6 non ovig ♀♀(21-31mm, mean 24.7); 2 mancas (7.0, 7.7mm), subsampled from c.200 specimens, data as for holotype (QM W17468).

Other Material: 200 specimens, topotypic series, same station as holotype, (QM W17471, NMV J27477, San Diego Natural History Museum). 4♂♂, 38♀♀, as for holotype, but 28 Apr 1989, 450m (QM W17469). 200+ specimens, as for holotype, but 29 Apr 1989, 300m (QM W17470). 93 specimens (mostly immature) outer barrier reef, between Rasch Pass and Wongat Is., 5°8.7'S, 145°49.7'E, 26-27 Jan 1990, 240m depth, coll. J.K. Lowry, J. Mizeu, J.D. Thomas (AM P40160).

Description

Body about 2.6 times as long as wide; pereonite 1>2=3<4=5<6>7. Pleonite 1 largely concealed by pereonite 7, epimera of pleonite 3 with posterior margin acute, with 3 longitudinal carina, medial one of which is provided with long setae; posterior margins of pleonite 4 epimera rounded, with very weak longitudinal carina. Pleotelson with lateral margins convex, converging to acute apex either side of which are 6 stout spines set amongst single row of PMS; spines restricted to distal third of pleotelson; proximal half (0.48) of lateral margin without PMS.

Cephalon with anterior submarginal furrow, dorsal interocular furrow running along top of eyes, but not extending beyond eyes. Antennule peduncle article 1 longest, 2 shortest; 4th short terminal article present; flagellum composed of about 32 articles, 1.5 times as long as peduncle, extending to anterior of pereonite 1. Antenna flagellum with about 60 articles, extending to anterior of pereonite 6. Frontal lamina as for genus. Mandible spine row with 19 spines; molar process with 27 spines interspersed with stout serrate setae; palp article 2 longest, with dense setose fringe on outer distal margin; article 3 lateral margin with continuous setae. Maxilla with 10 and 13 setae on lateral and middle lobes respectively; medial lobe with 1 large and 4 smaller circumplumose setae; anterior to these are two ranks of setae, posterior rank of 13 simple setae, anterior rank of 8, distal 5 of which are long. Maxilliped palp with simple setae on lateral margins of articles 3-5, PMS on article 2; articles 2-5 with about 15, 35, 20 and 11 lateral setae respectively; medial margins of articles 2-5 with about 19, 20, 12 and 12 setae respectively; article 5 with some serrate setae; endite with 6 long plumose setae.

FIG. 2. *Aatolana rapax* sp.nov. All figs of♂paratype 32.2mm, except N. A, maxilliped; B, distal margin, maxilliped palp article 5; C, distal margin, antennule peduncle; D, antennal flagellum, articles 23-27; E, maxilliped endite; F, pereopod 1; G, pereopod 2; H, pereopod 7; I-L, pleopods 1,3,2,5 respectively; M, pleopod 2 peduncle lateral margin; N, apex of appendix masculina,♂31.5mm (An = anterior margin, Po = posterior margin).

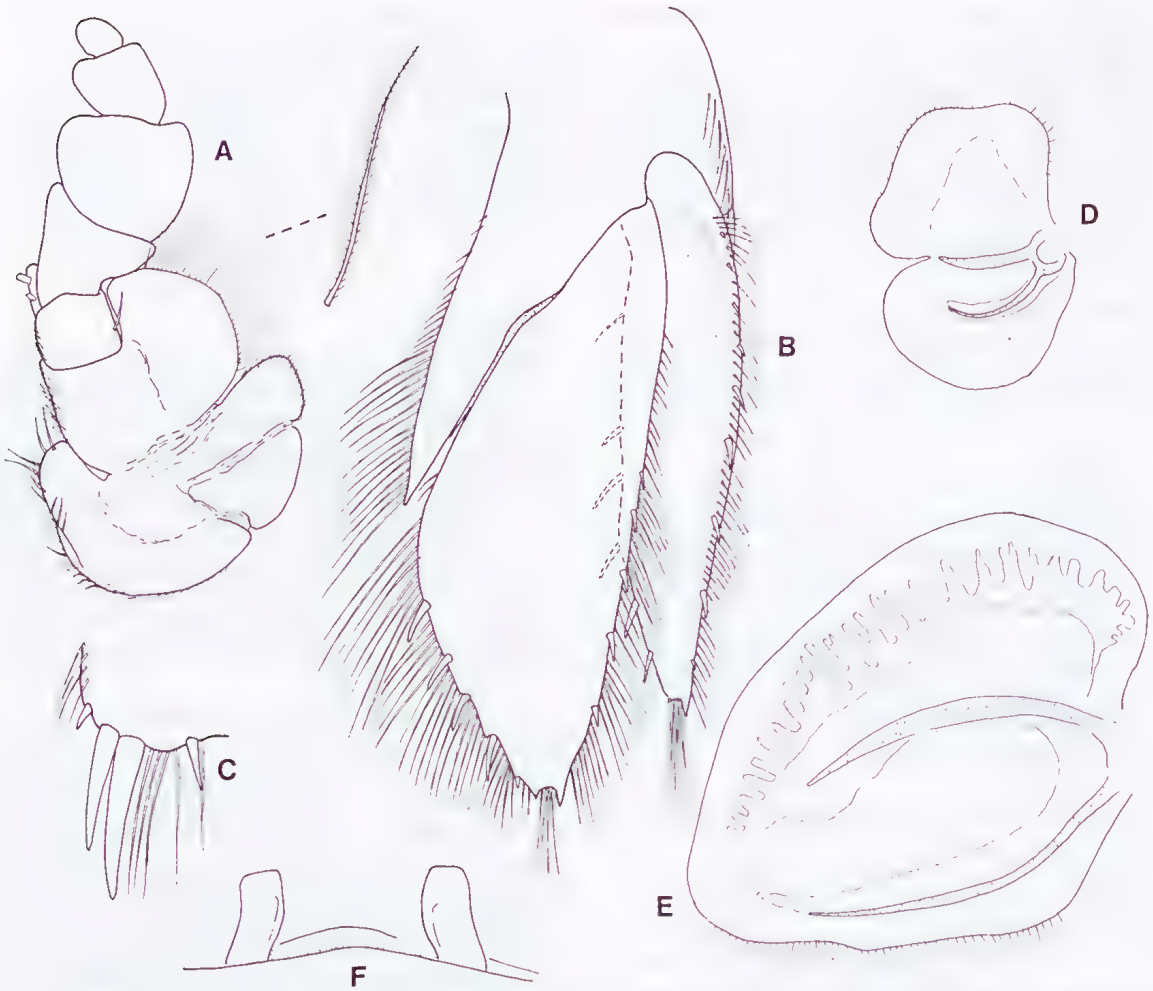
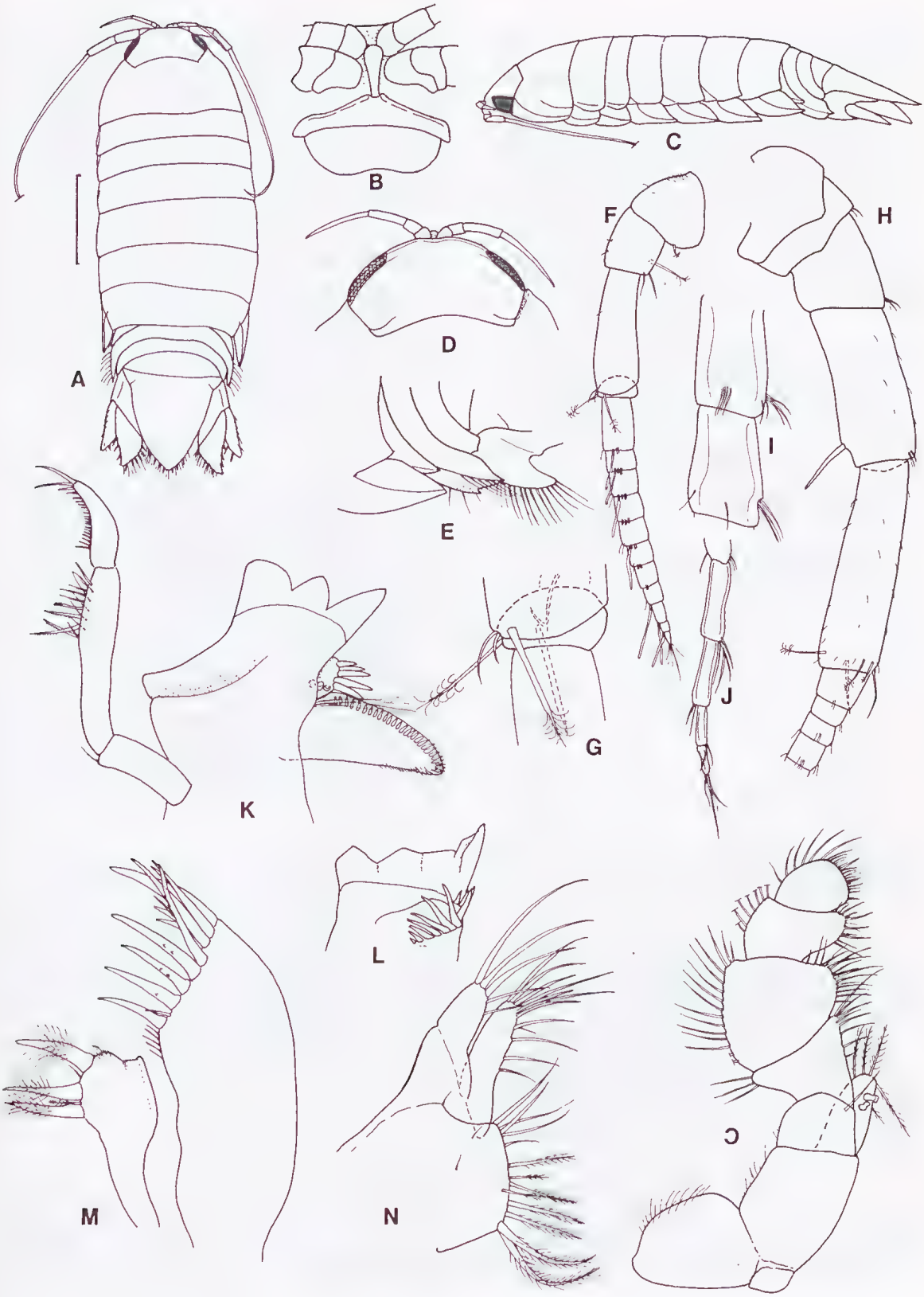


FIG. 3. *Aatolana rapax* sp.nov. A, D, E, ovig. ♀ paratype 29.4mm. A, maxilliped, showing lobes; D, oostegite 1; E, oostegite 5; B, uropod, ♂ paratype 32.2mm; C, ventrolateral angle, uropod peduncle, ♂ 32.2mm; F, penes, *in situ*, holotype.

Pereopod 1 basis with 5 setae at posterodistal angle; ischium with 6 setae at anterodistal angle; merus with 9 tubercular spines on posterior margin, 5 short simple setae at anterodistal angle; carpus with single spine on posterior margin; propodus with 3 spines on palm, 4th larger spine opposite base of dactylus. Pereopod 2 longer than 1; ischium with 6 long spines anterodistal angle, 2 robust spines posterodistal angle; merus with indented posterior margin, proximal portion with 6 stout spines, anterior portion with 2 large stout and 1 acute spine and 6 stout spines at anterodistal angle; carpus with 4 spines at anterodistal angle; propodus with 3 small spines, 4 spine at anterodistal angle; propodus with 3 small spines, 4th spine opposite base of dactylus. Pereopod 7 basis with fringe of setae on anterior margin and median carina; posterior margin of ischium with 3 clusters of short setae, 4 large spines at posterodistal angle; merus and carpus with cluster of spines on posterior margin and posterodistal angle; ischium-carpus with clusters of spines at anterodistal angles only; propodus with 3 pairs of spines on posterior margin.

FIG. 4. *Plakolana accola* sp.nov. A-E, holotype, ♂ remainder paratype 9.3mm. A, dorsal view; B, frons; C, lateral view; D, cephalon; E, pleonites, lateral view; F, antennule; G, distal margin, antennule peduncle; H, antennal peduncle; I, antenna, flagellum articles 9 and 10; J, antenna, flagellum terminal articles; K, right mandible; L, left mandible, incisor and spine row; M, maxillule; N, maxilla, O, maxilliped. Scale represents 2.0mm.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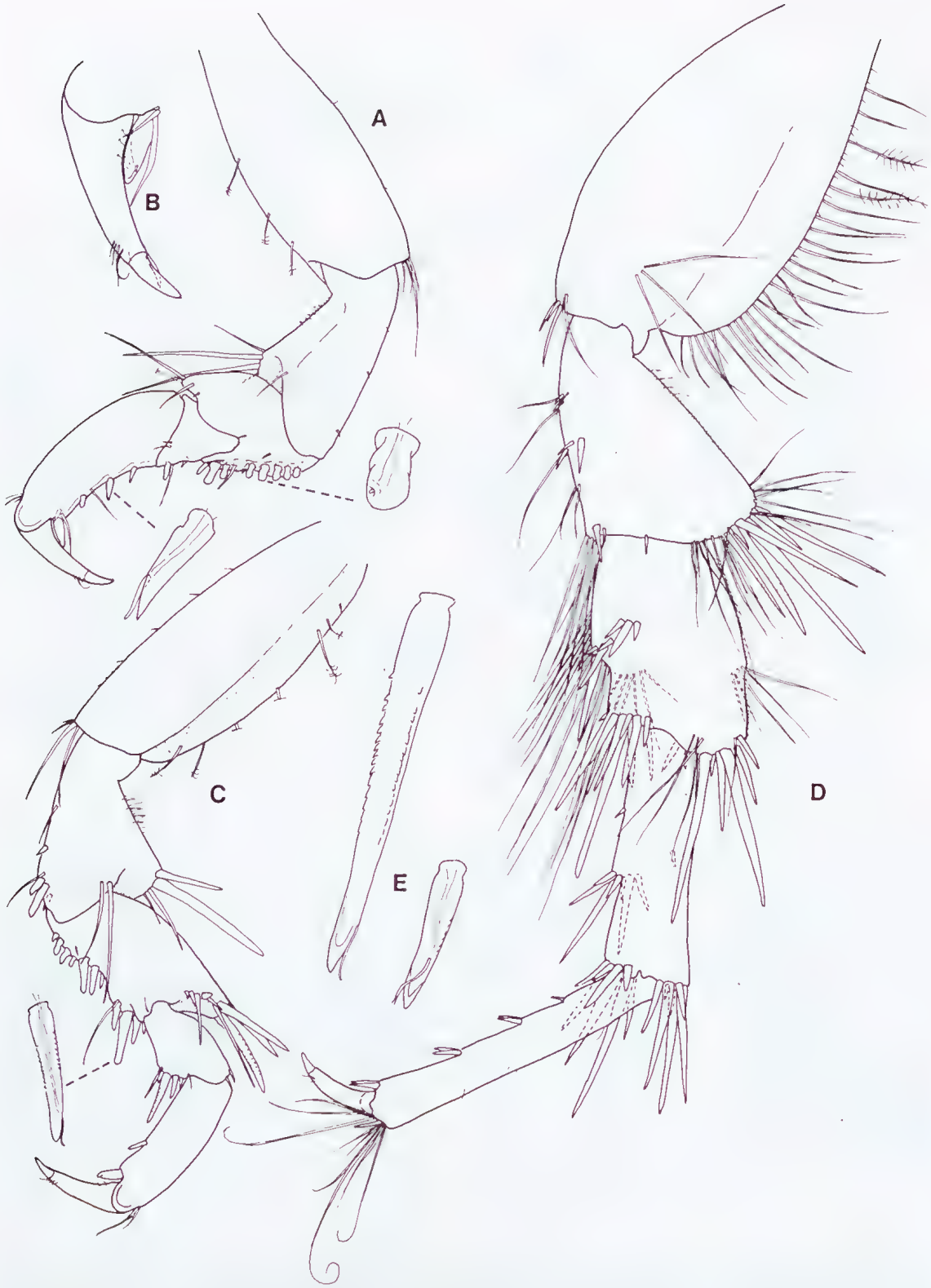


FIG. 5. *Plakolana accola* sp.nov. All figs of ♂ paratype 9.3mm. A, pereopod 1; B, dactylus, pereopod 1; C, pereopod 2; D, pereopod 7; E, spines from posterodistal angle of merus.

Pleopods as for genus. Appendix masculina with apex bent medially. Uropod exopod distinctly shorter than endopod, apex sub-bifid, lateral process prominent; lateral margin with 8-10 spines, medial with 5 spines set amongst PMS. Endopod lateral margin straight, with 5 spines, PMS for about 0.75 distal margin; medial margin with 5 spines set amongst PMS; apex sub-bifid, small spine set medially to apex.

Female. Similar to male but for: maxilliped with lamina vibrans (3 plates); pleopod endopod lobes slightly larger. Oostegites on coxae 1-5, largely overlapping; embryos retained with single large cavity formed by indentation of ventral body surface in body. Female of 29mm contained 28 ova, measuring 2.5-2.8mm in diameter.

Colour. Pale tan with abundant small reddish brown chromatophores giving a rusted appearance in life; eyes black.

Size. Males 19-32mm, non-ovigerous females 21-31mm, ovigerous females (4 specimens measured) 29-32mm. Two mancas, with pereopod 7 not present, measured 7.0 and 7.7mm.

Variation. Males, females and mancas present uniform appearance, but many specimens had malformed uropods and pleotelson. The spine counts presented here are based on 20 specimens, but damaged specimens have been omitted. Telson (n=17) with 6+6 spines (41.2%), 6+7 spines (29.4%) or 7+7 (29.4%). Exopod (n=38) lateral margin with 9 (47.4%), 8 (21.1%) or 10 (15.8%) spines; medial with 5 (94.7%) spines. Endopod (n=36) lateral margin with 5 (44.4%), 6 (41.7%) or 7 (5.6%) spines; medial margin with 5 (11.0%), 6 (63.9%) or 7 (27.8%) spines.

Remarks

This species is readily identified and distinguished from *A. schioedtei* by the pleotelson spines being restricted to the posterior third of the pleotelson, uropod lateral margins being straight not sinuate, posterior margin of pleonite 4 being rounded not acute and in lacking an entire dorsal interocular furrow. *Aatolana rapax* never has the dorsal surface of the pleotelson setose, which occurs in large males of *A. schioedtei*.

Plakolana gen.nov.

Body smooth, unornamented. Cephalon anterior margin medially indented, without rostral point. Pereonite 1 about twice as long as 2; pleonite 1 partly or wholly concealed by pereonite 7. Pleonite 3 with epimera prominent, with postero ventral incision; longitudinal carina with row of setae; extends posterior to pleonites 4 and 5. Telson with prominent spines and PMS.

Antennule peduncle articles 1 and 2 subequal in length, article 3 slightly longer than combined lengths of articles 1 and 2. Antenna with articles 1-3 short, 4 and 5 long, with article 5 longest. Frontal lamina slender, elongate, about 5 times longer than basal width. Mandibles with prominent spine row and molar process. Maxillule lateral lobe with stout spines on gnathal surface, medial lobe with 3 stout circumplumose spines. Maxilla with all lobes well developed. Maxilliped palp articles 2-5 with both margins setose; endite with 2 coupling hooks and prominent plumose setae.

Pereopods 1-3 with long spines at anterodistal angles of ischium and merus; pereopods 4-7 with ischium, merus and carpus, expanded, markedly flattened, abundantly provided with long spines, and long simple setae on anterior margin of basis, and posterior margins ischium and merus. All pereopods with slender secondary unguis on dactylus. Penes opening flush (or nearly so) to ventral surface of sternite 7.

Pleopod 1 peduncle quadrate, slightly longer (1.2) than wide; pleopod 2 appendix masculina attached basally. PMS present on all rami except the endopod of pleopod 5. Uropod peduncle with prominent row of simple setae along lateral margin.

Female: Maxilliped with lamina vibrans, in ovigerous specimens. Brood pouch composed of oostegites arising from coxae 1–5.

Type Species

Plakolana accola sp.nov., here designated.

Etymology

From the Greek *Plakos* ('anything flat and wide') combined with *-lana*. Gender is feminine.

Remarks

The genus is characterized by having flattened and densely spined and setose posterior pereopods, slender secondary unguis on the dactylus, the unique shape of pleonite 3 (with an a cute posterior point and ventrolateral incision), the elongate frontal lamina and the quadrate peduncle of pleopod 1. The flattened basis pereopaods 4-7 with a row of simple setae along the anterior margin, is the only character that can be recognized as a potential unique apomorphy. Nonetheless the combination of characters delimits the genus.

Species of *Cirolana* never have flattened posterior pereopods, nor pereopods with abundant setae or elongate spines, and the peduncle of pleopod 1 is about twice as wide as long; in

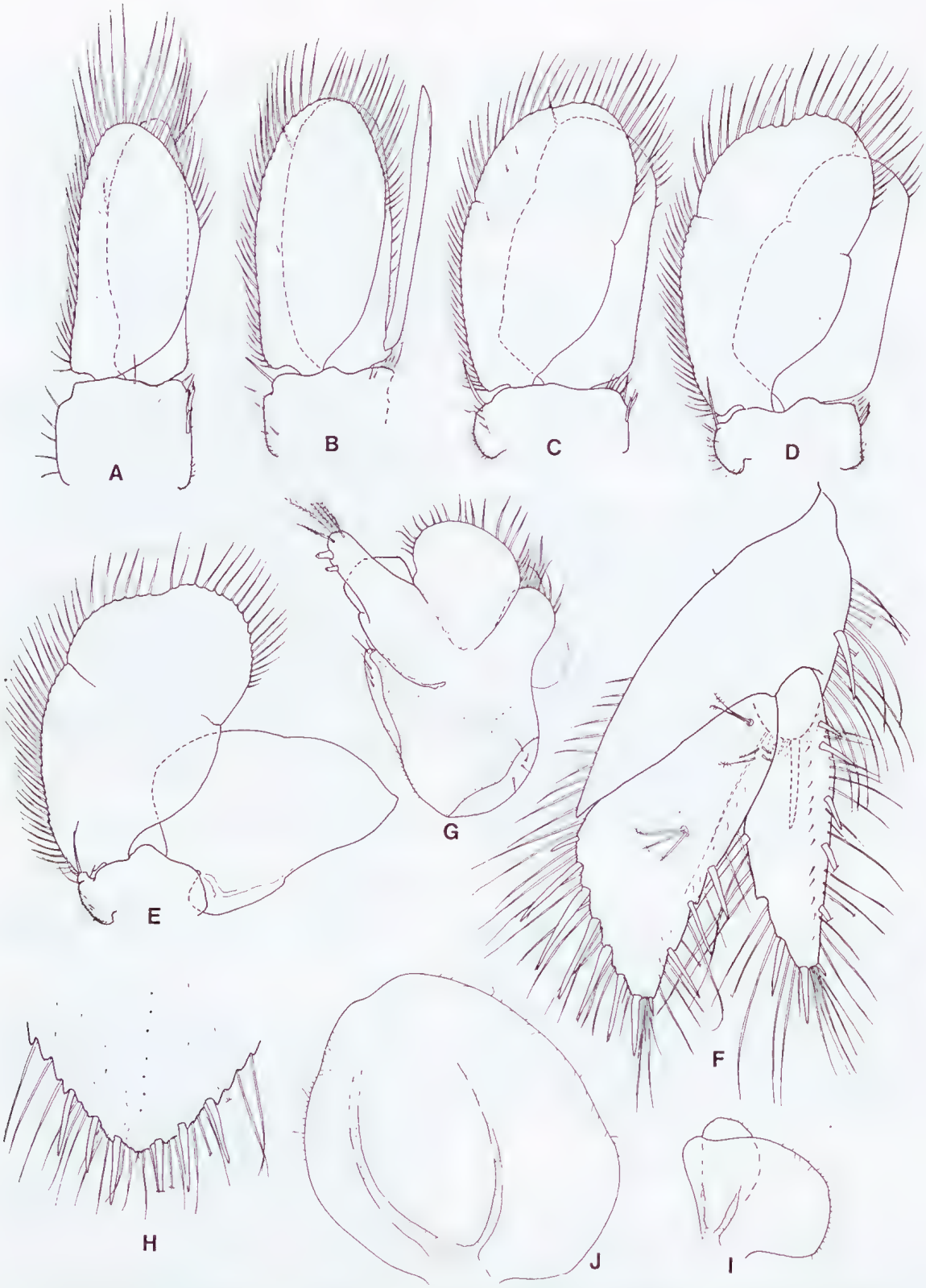


FIG. 6. *Plakolana accola* sp.nov. G, I, J, ♀paratype 10.5mm, remainder ♂ paratype 9.3mm. A-E, pleopods 1-5 respectively; F, uropod; G, maxilliped, showing lobes; H, pleotelson apex; I, oostegite 1; J, oostegite 5.

Cirolana the cephalon has a rostral point or smoothly rounded, but never medially indented. Those species that do show some of these character (see below) are in need of redescription and their generic placement reassessed.

DISTRIBUTION

The genus is currently known from the western South Pacific.

OTHER SPECIES

Plakolana binyana (Bruce, 1991). comb.nov. Southeastern Australia.

Plakolana nagada sp.nov. Madang, Papua New Guinea.

Plakolana sp. (as *Cirolana* sp. Bruce, 1986). Eastern Australia. Known from a single immature specimen.

It is possible that *Cirolana bougartii* Kensley, 1984 belongs in *Plakolana* because the morphology of the antennule, frontal lamina, pereopods and pleopods all agree with the generic diagnosis. Characters that differ include the anterior margin of the cephalon being apparently smoothly rounded (possibly due to the perspective of the figure), pleonite 1 is largely visible, and the pleotelson and uropods are not described as having spines. This species needs further examination to assess its correct generic placement. Similarly *Cirolana stebbingi* Nierstrasz, 1931 shows a similar pleon, antennule, pereopod and pleopod morphology, and also needs to be described in detail before it can be assigned to the correct genus.

AFFINITIES

The pereopod morphology, smooth body surface, elongate pleopod 1 peduncle, and frontal lamina shape suggest that this genus is closest to *Politolana* Bruce, 1981. *Politolana* however differs in having the anterodistal margin of the ischium and merus of pereopod 1 strongly produced, in having the basis anterior margin without setae and furthermore lacks the long spines of *Plakolana*. The appendix masculina is sword shaped and sub-basally attached. In *Politolana* the antennal morphology, with peduncle articles 1 and 2 short, 3-5 long, is more similar to that of *Natatolana* than to *Plakolana* which has antennal peduncle articles 1-3 short, 4 and 5 long.

KEY TO THE SPECIES OF *PLAKOLANA*

1. Frontal lamina widest anteriorly; uropod endopod spines long (15-35% length of endopod); uropod endopod distally narrowed, medial margin approximately straight 2

   Frontal lamina with straight lateral margins; uropod endopod spines short (less than 12% length of endopod); uropod endopod distally wide, medial margin sinuate. 3

2. Antenna flagellum extending to pereonite 4 or 5; uropod endopod medial margin with 7 spines, distalmost spine about equal in length to adjacent spine. . . . . *P. accola*

   Antenna flagellum extending to pereonite 2 or 3; uropod endopod medial margin with 5 spines, distal most of which is twice as long as adjacent spine . . . . . *P. nagada*

3. Cephalon with complete dorsal interocular furrow; frontal lamina anteriorly rounded; pleotelson with 7* spines. . . . . *Plakolana* sp.

   Cephalon dorsal interocular furrow incomplete; frontal lamina distally acute; pleotelson with 4 spines . . . . . *P. binyana*

**Plakolana* sp. was described from a juvenile (Bruce, 1986: 143, fig. 96). In cirolanids pleotelson spines are nearly always paired, in which case the 'normal' spination for this species would be 6 or 8.

Plakolana accola sp.nov.
(Figs 4-6)

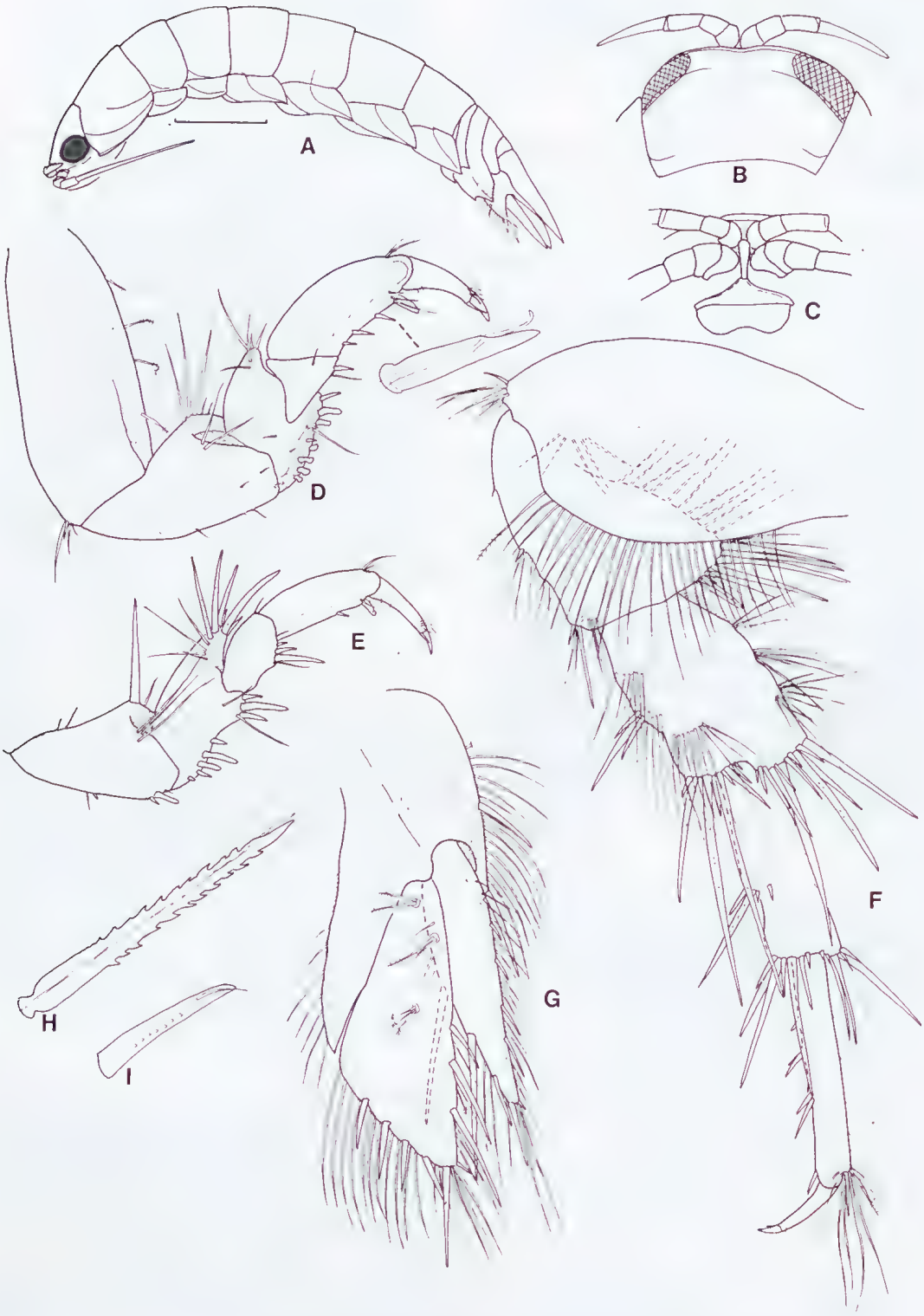
MATERIAL EXAMINED

HOLOTYPE: ♂ (9.5mm), off outer reef slope, south of Wongat Is., 5°08.4'S, 145°51.0'E, 29 Apr 1989, 300m depth, coll. N.L. Bruce & M. Jebb (QM W17993).

PARATYPES: 4♂♂ (9.3 dissected, 9.0, 7.8, 7.0mm), 9 ♀♀(10.5mm ovig, 10.5, 8.0, 8.0, 7.5, 7.0, 6.5, 6.5, 6.0mm), 3 imm (5.5, 5.0, 5.0mm), same data as holotype (QM W 17994-17996). 2♂♂(7.5, 6.8mm), ♀(7.0 non-ovig), as for holotype but 29 Apr 1989, 450m depth (NMV J27475). 9♂♂, 5♀♀, 8 mancas, off outer reef slope between Rasch Pass and Wongat Is, 5°8.7'S, 145°49.7'E, 26-27 Jan 1990; 440m depth, coll J.K. Lowry, J. Mizeu, and J.D. Thomas (AM P40161; 1♂, 1♀ San Diego Museum).

DESCRIPTION

Body about 2.7 times as long as wide. Cephalon with anterior submarginal furrow, dorsal interocular furrow absent. Pereonite 1>2=3<4<5=6>7. Coxae of only pereonites 7 clearly visible in dorsal view. Pleon short, ca. 10% of BL, all of pleonite 1 and most of pleonite 2 concealed by pereonite 7. Pleotelson about as long as wide, lateral margin convex, converging smoothly to subacute apex; posterior margin with 6 acute spines and PMS.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Antennule peduncle article 3 longer than lengths of article 1 and 2 combined; flagellum composed of 11 articles, article 1 longest, and extending to anterior of pereonite 1. Antenna with flagellum of 32 articles, extending to anterior of pereonite 5. Frontal lamina anteriorly widest, with anterior margin rounded; about 2.5 times as long as maximum width. Mandibles with 8 (right) or 11 (left) spines on spine row; molar process with about 28 teeth; palp article 2 with about 11 simple and 4 serrate spines; article 3 with 20 spines. Maxilla with 11 spines on gnathal surface setae on lateral and middle lobes respectively; medial lobe with 7 plumose setae (proximal) and 5 simple seta. Maxilliped with simple setae on lateral shorter, those of article 5 serrate and simple; endite with 5 long circumplumose setae.

Pereopod 1 with 4 setae at posterodistal angle of basis; 3 terminally plumose setae on anterodistal margin; ischium posterior margin with 2 small spines, anterodistal angle with 3 long setae; merus with 7 blunt tubercular spines and 2 acute spines on posterior margin, anterodistal angle with 3 setae; carpus posterior margin with 2 spines and single seta; propodus with 3 spines on palm, 4th large spine opposing base of dactylus; dactylus without distinct secondary unguis. Pereopod 2 with long spines at anterodistal angles of ischium and merus; ischium posterior margin with 2 setae and 1 acute spine, distally with 2 blunt spines; merus posterior margin with 1 long seta and 1 stout spine; carpus with 4 spines, 1 long, and 2 setae; propodus with 1 spine on palm, 1 opposing dactylus. Pereopod 7 basis with margins convex, posterior margin with about 28 feebly PMS; ischium carpus with large clusters of long spines and simple setae at distal margins; posterior margin ischium and merus with 2 and 1 cluster of spines, merus with long setae; propodus with 3 groups of paired spines and a single spine proximally; anterodistal angle with long setae.

Pleopod 3-5 exopods with partial suture only. Uropod peduncle with prominent row of setae on lateral margin; with single lateral spine and 2 spines at distoventral angle; exopod lateral margin with 5 prominent and 1 small subapical spine, medial margin with 4 spines, distal spine not much larger than adjacent spine; endopod lateral margin weakly sinuate, with 3 prominent spines, longest 18% length of lateral margin, and 1 small subapical spine, medial margin with 7 spines, distal spine not much larger than adjacent spine. All margins with PMS, except proximal half (0.45) of endopod lateral margin without setae.

Female: Similar to male; oostegites on coxae 1-5; maxilliped with lamina vibrans (3 plates). Females with embryos not observed.

Colour. White to translucent in life and alcohol; chromatophores absent. Eyes pale, reddish brown to yellow.

Size. Males 7.0 - 9.5 (mean = 8.1, *n*=7), females 6.0-10.5 (mean = 7.8, *n*=10), mancas up to 5.5mm.

Variation. Pleotelson and uropod spine counts were near constant. Exopod (*n*=23) lateral margin with 5 prominent spines (95.6%), medial margin with 4 spines (64.7%) or 5 (29.4%). Endopod (*n*=23) lateral margin with 3 prominent spines (100%), medial margin with 6 (8.7%), 7 (86.9%) or 8 (4.3%).

Remarks

Plakolana accola can be distinguished from others of the genus by the short pleon which has segment 1 and most of 2 concealed by pereonite 7. *P. binyana* from southern Australia has the frontal lamina with a narrow anterior margin and broader uropods which have far shorter spines. *P. nagada*, which occurs in shallow water within the barrier reef system at Madang, is readily distinguished by a longer pleon, longer spines on the uropods, and by having the distalmost spine on the medial margin of each uropod ramus far longer than the adjacent spine.

Distribution

Outer reef slope at Madang, between 300 and 450m depth.

Etymology

Accola is a Latin word meaning neighbour.

Plakolana nagada sp.nov.
(Figs 7, 8)

Material Examined

Holotype: ♂ (6.9mm), east of CRI jetty, Nagada Harbour, 5°09.6'S, 145°48.7'E, 2 Feb 1990, 16m depth, soft mud bottom, coll. J.K. Lowry and J.K. Elliot (AM P41015).

Paratypes: ♂ (7.8mm, dissected), 5♀♀ (8.0 dissected, 7.5, 7.3, 7.2, 7.2mm), imm (4.9mm), same data as holotype (AM P40172). ♀ (7.1mm, ovig), south of

FIG. 7. *Plakolana nagada* sp.nov. A-C, holotype, remainder ♂ paratype 7.8mm. A, lateral view; B, cephalon, C, frons; D, pereopod 1; E, pereopod 2; F, pereopod 7; G, uropod; H, spine, distal margin of merus; I, short spine, anterodistal angle of carpus. Scale represents = 1.0mm.

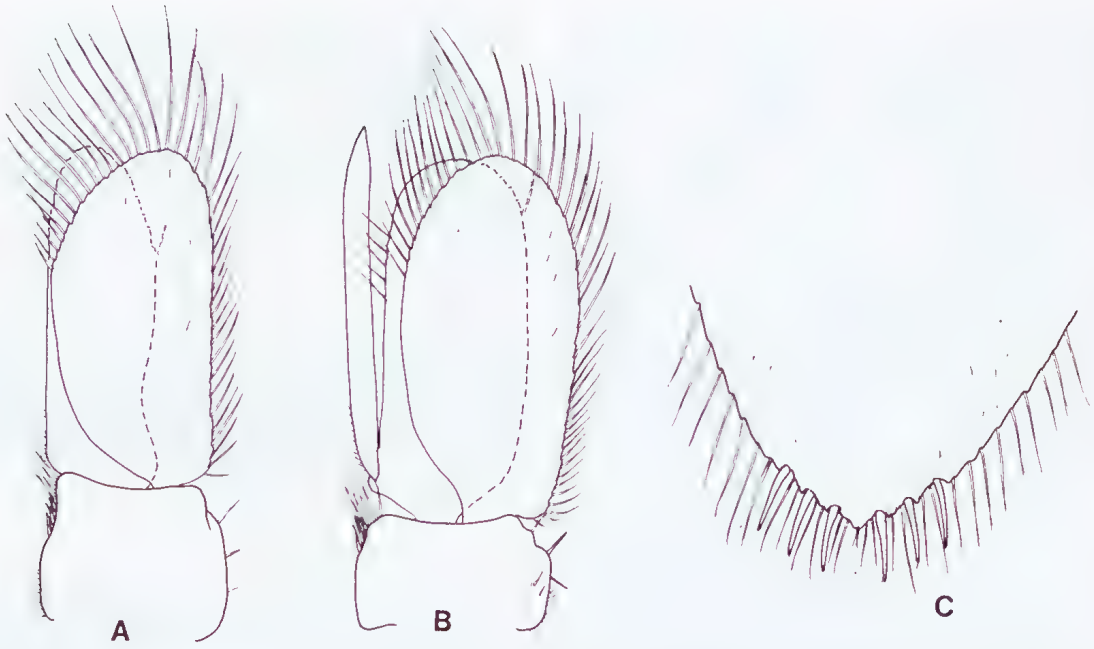

FIG. 8. *Plakolana nagada* sp.nov. All figs of ♂ paratype 7.8mm. A, pleopod 1; B, pleopod 2; C, pleotelson apex.

Tripod Reef, 5°09.7'S, 145°51.3'E, 30 Apr 1989, 22m depth, on sand, coll. N.L. Bruce (QM W18001).

DESCRIPTION

Pleon about 12.5% BL, pleonite 2 largely visible. Pleotelson with 6 spines.

Antenna flagellum extending to posterior of pereonite 3.

Pereopod 1 merus posterior margin with 6 blunt spines and 2 short acute spines. Pereopod 2 merus posterior margin with 1 long seta and 8 stout spines. Pereopod 7 merus with 3 clusters of setae on anterior margin; posterior margin with 2 ranks of simple setae.

Uropod exopod lateral margin with 5 prominent and 1 small subapical spine; medial margin with 4 spines, proximal two longest, distal spine distinctly longer than adjacent spine. Endopod lateral margin with 3 prominent and 1 small subapical spine; 2 longest spines are 32 and 35% length of lateral margin; medial margin with 5 spines, distalmost spine about twice as long as adjacent spine.

Colour. Pale brown in alcohol; eyes pale brown.

Size. Adults 6.9 - 8.0mm.

Variation. Pleotelson and uropod spine counts are near constant. Exopod lateral margin with 5 large and 1 small (100%); medial margin with 4 spines, 3 once. Endopod lateral margin 3 large spines and 1 small (86.6%) or with 2 large spines (13%); lateral margin with 5 (54.5%) or 6 (45.5%) spines (n=15 for all percentages). Pleotelson posterior margin with 6 (62.5%) or 5 (37.5%) spines (n=8).

REMARKS

Plakolana nagada is very similar to *P. accola*, but differs both in habitat (inshore, shallow sedimentary bottom compared to deeper reef slope) and numerous morphological features.

P. nagada in the first instance has much longer pereopod and uropod spines, and also has more of the pleon visible. Specifically the two species can be separated by *P. nagada* having most of pleonite 2 visible, 5 spines on endopod medial margin (vs 7), the terminal spines on the endopod and exopod medial margins being far longer than the adjacent spine, and the spines on the lateral margin of the endopod being much longer (32-35% ramus length vs 18% in *P. accola).*

DISTRIBUTION

Shallow muddy and sand bottoms within the barrier reef at Madang; recorded depths 16 and 22m.

ETYMOLOGY

The epithet is taken from the type locality, and treated as a noun in apposition.

ACKNOWLEDGEMENTS

This contribution was made possible by a Christensen Research Institute Fellowship, for which I thank the Christensen Fund. I also thank Dr Matthew Jebb for his considerable field assistance.

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FIRST RECORD OF CTENOPHORE *COELOPLANA* (*BENTHOPLANA*) *METEORIS* (THIEL, 1968) FROM AUSTRALIA. *Memoirs of the Queensland Museum 33(1): 16. 1993*:- There are only two records of benthic ctenophores (Ctenophora: Platyctenida) from Australian waters: *Coeloplana* sp. and *C.* cf *willeyi* Abbott, 1907 (Stephenson et al., 1931; Smith & Plant, 1976). I record here a third species, *Coeloplana* (*Benthoplana*) *meteoris* (Thiel, 1968), previously known from Somalia, east Africa (08°26.2'N, 50°20.2'E) (Thiel, 1968) and NW Madagascar (13°24'40-13°35'15"S, 47°48'50-48°19'10"E) (Fricke & Plante, 1971). The specimens were collected while diving at 12-13m depth in Pioneer Bay, Orpheus Island, NEQ (18°36'S, 146°29'E). Two specimens were preserved (Queensland Museum G35888). The following description is based primarily on living animals in which taxonomic features are clearest.

The animals were living free on terrigenous muddy-sand. They had a characteristic body profile with erect tentacular horns (see Thiel, 1968, figs 1,2; Fricke & Plante, 1971, pl.1). The aboral surface was covered by a yellowish-white reticulate pattern. Fine red pigment occurred on the aboral surface above the meridional canals, around the tentacle sheaths and marginal ampoules. One live specimen, when expanded on glass, measured 36×31mm. The preserved specimens measure 8×10 and 10×16mm.

The apical organ had four polar fields, which were multiply branched (see Fricke & Plante, 1971, fig. 3). The fields did not contract, however, as observed by those authors.

Tentacles were typical with a primary axis and tentilla. They extended from beneath the tip of the tentacular horn, i.e., the opening of the tentacle sheath was oral.

The preserved specimens are folded along the tentacular axis; a faint crease runs along the oral surface from the mouth to the base of the tentacular horns, but no oral groove or oral lappets were seen.

The following description of the gastrovascular system uses the terms of Thiel (1968). Radial canals gave rise on either side to 2 pairs of adradial canals that led directly to the meridional canals. There were 3-4 digitate to trifid aboral papillae over each of the meridional canals. A pair of subparallel tentacular canals ran on either side of the tentacle sheath, arising beyond the distal adradial canals. The peripheral gastrovascular system branched dichotomously to form a complex network, best developed on the oral surface.

Cydippid larvae were found next to the meridional canals (the specimens were collected in January). Peripheral sacs were each connected by a transparent tube to a marginal pore. These seem to be testicular ampoules (see Fricke & Plante, 1971).

Body profile, marginal position of tentacle sheath openings and variable aboral papillae are consistent with *Vallicula* Rankin, 1956 and some species of *Coeloplana* Kowalevsky, 1880 as defined by Fricke (1970), Harbison & Madin (1982) and Rankin (1956). However, I did not see the oral lappets, oral groove, spherical vesicle of the gastrovascular system or additional cross-piece of the tentacular sheath that characterize *Vallicula*.

Of the 21 nominal species of *Coeloplana* (Fricke, 1970), three have a gastrovascular system similar to that in my specimens: *C. perrieri* Dawydoff, 1938, *C. mesnili* Dawydoff, 1938 and *C. meteoris* Thiel, 1968 (Thiel, 1968; Fricke & Plante, 1971). All were reported as free-living (*C. mesnili* in the plankton, *C. perrieri* on rocks and seagrass, *C. meteoris* on soft-sediment). The present specimens differ from *C. mesnili* and *C. perrieri* (Dawydoff; 1938a,b) in body profile, position of openings of the tentacle sheath and testes, colour pattern, structure of the apical organ and aboral papillae. They conform well with *C. meteoris* in (1) the free-living habit on soft-sediment, (2) high body profile with tentacular horns, (3) oral openings of the tentacle sheath, (4) distinctive apical organ with four polar fields, (5) tentacular canals bifurcating beyond the distal adradial canals, (6) colour pattern, (7) complex aboral papillae, and (8) marginal position of ampoules (otherwise known only from *Ctenoplana* (*Diploctena*) *neritica* Fricke & Plante, 1971). This combination of features was so distinctive that Fricke & Plante (1971) created a new subgenus, *Benthoplana*, for *C. meteoris*.

This record considerably extends the range of *C. meteoris*. Fricke & Plante (1971) showed it can be abundant (up to 64/m^2). The paucity of published records probably reflects the lack of direct observations in soft-sediment habitat.

Specimens were collected during a study on soft-sediment epibenthos with Dr R.A. Birtles (James Cook University), funded by an Australian Marine Sciences and Techology grant. I thank Drs A. Birtles and C. Wallace for their comments.

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Peter Arnold, Museum of Tropical Queensland, 70-84 Flinders St, Townsville, Queensland 4810, Australia; 15 October, 1992.

NEW TEMNOCEPHALANS (PLATYHELMINTHES): ECTOSYMBIONTS OF FRESHWATER CRABS AND SHRIMPS

L.R.G. CANNON

Cannon, L.R.G. 1993 06 30: New temnocephalans (Platyhelminthes): ectosymbionts of freshwater crabs and shrimps. *Memoirs of the Queensland Museum* **33**(1): 17-40. Brisbane. ISSN 0079-8835.

Six new species of *Temnocephala* are described from freshwater crabs and shrimps from Queensland, *Temnohaswellia* Pereira & Cuocolo, 1941 is re-erected for two new species with 6 tentacles and *Achenella* n. gen. is proposed for two new species of worms with only one pair of testes. This is the first time temnocephalans have been reported from crabs and shrimps in Australia. □ *Temnocephala, Temnohaswellia, Achenella , ectosymbiont, crab, shrimp.*

Lester R.G. Cannon, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; *2 November, 1992.*

Temnocephalans are small ectosymbiotic flatworms which are known from a variety of freshwater invertebrates from mainly South America and Australia. Their taxonomic status has shown some variation (Williams, 1981), but they are generally considered to be close to the dalyellioid turbellarians. The Australasian region seems the centre of diversity (Cannon, 1991), but here the diversity of hosts recognised has been low, i.e., they have been reported almost exclusively from crayfish of the family Parastacidae. Crabs and shrimps have been reported as hosts in southern Asia and South America; however, this is the first such report from Australia.

Crabs and shrimps were trapped or collected in dip nets from streams and ponds throughout eastern Australia. Hosts were retained for short periods until the hosts could be examined in the field or laboratory with a dissecting microscope and the worms removed into clean water. Worms were fixed when possible in 10% cold buffered formalin, AFA (alcohol, formalin and acetic acid), SUSA or Bouin's fluid: some were obtained from hosts fixed in 70% alcohol or from hosts killed by near boiling water. Whole mounts were stained with Mayer's haemalum or Harris' haematoxylin and mounted in Canada balsam. Serial sections were obtained from worms embedded in 56°C Paraplast and cut at 5-7μm and stained with Mayer's haematoxylin and eosin, though occasionally Mallory's trichrome was used.

Descriptions were prepared with the aid of DELTA (Dallwitz & Paine, 1986). Over 130 characters were designated, though not all were applicable to all descriptions, e.g. egg capsule characters were not included if egg capsules were not found. With limited material of some species and variation in the quality of fixation dependent upon the immediacy of treatment some characters are included as 'inconspicuous', '(absent?)' or simply qualified with '(?)'. All measurements were obtained with the aid of a camera lucida. Material is deposited in the collections of the Queensland Museum (QM) and wholemounts are designated (W) and serial sections (LS, TS or FS -longitudinal, transverse or facial sections: the number of slides in the series given in [ ]).

Abbreviations used in figures: c cirrus, dg disc glands, e eye, es ejaculatory sac, ex excretory ampulla, g gut, ga genital atrium, gc genital capsule, gp gonopore, Hc Haswell's cells, og ootype gland, ov ovary, ph pharynx, plg postero-lateral glands, pr prostate, rg rhabdite glands, ro rosette organ, sg shell glands, sr seminal receptacle, sv seminal vesicle, t testis, v vagina, vit vitellaria, vitd vitelline duct, vr vesicula resorbens.

TERMINOLOGY

Hickman (1967) drew attention to the variety of names used for various parts of the reproductive organs of temnocephalans. I happily accept the term vesicula resorbens (not resorbiens) for this structure described in detail by Haswell (1924). Earlier I have tried to provide a consensus regarding the terminology relating to all turbellarians (Cannon, 1986). Within the male temnocephalan I agree with Haswell (1893) and Baer (1953) that the swollen part of the system storing sperm prior to release is appropriately called the seminal vesicle. The ejaculatory duct leaves the seminal vesicle distally and enters the (usually muscular) base of the intromittent organ. Haswell

(1893) called this muscular base the cirrus bulb, but since this is where the prostate glands join the ejaculatory duct and surround it 'prostate bulb' (or simply 'prostate') is the most appropriate functional term. The prostate is sometimes no wider than the sclerotic base of the male organ, but may be a much enlarged bulb.

As Baer (1953) pointed out, Australian species of temnocephalans also have an additional sac, evidently absent from South American species. This is variably developed: in some it is a discrete sac or vesicle opening, via a narrow duct, into the prostate adjacent to the ejaculatory duct; in others it is merely a proximal extension from the prostate beyond the ejaculatory duct entrance. Haswell (1893) called this the ejaculatory sac, a term I accept. Hickman (1967) called it a prostate vesicle mistakenly attributing this term to Baer (1953) who called such a structure in *Dicerato-cephala boschmai* a prostate, but said 'elle est sans doute homologue de la vesicle ejaculatrice des autres Temnocephales'. This sac is frequently empty or contains only a few sperm: it does not contain prostatic secretion.

The male intromittent organ in most temnocephalans consists of a hard sclerotic tube the terminal part of which has spines or more often rows of spinelets which are eversible. The terminal part may or may not be enlarged. Haswell (1893) called the organ a cirrus and the terminal part the introvert. Cirrus is the appropriate term for a spiny eversible male organ. The basal rigid section could be considered a stylet, but is here called the shaft, and the term 'cirrus' of Haswell is accepted here, not 'penis' as used by Hickman (1967).

Finally, in many temnocephalans there are distinctly staining cells anterior to or adjacent to the brain. Haswell (1893) first referred to them as 'problematic cells'. They have also been called 'schokoladenbraune Drüsen' (see Cannon, 1991). Hickman (1967) figures and describes these cells which he says may be paranephrocytes, though cautiously, as these latter are wandering cells: the cells in question are constant in position. There are often two pairs and their position near the brain suggests they may be neurosecretory. Until a function can be ascribed I propose to call them Haswell's cells.

Family TEMNOCEPHALIDAE Monticelli, 1899

Temnocephala Blanchard, 1849

Generic diagnosis. Temnocephalidae with five anterior tentacles, a posterior adhesive disc and paired lateral testes.

Temnocephala athertonensis n.sp.
(Figs 1,11a-c)

MATERIAL EXAMINED

HOLOTYPE: ex carapace of *Holthuisana agassizi* (Sundathelphusidae), Rocky Ck, nr Carbeen (17.11.2°S, 145.26.8°E), 26 Sep. 1990, L. Cannon & K. Sewell, Hot water/AFA/Hx GL14562 (W).

PARATYPES: same data as holotype, AFA/Hx GL14563-7 (W); Hot water/Bouin's/H&E GL14569 (LS[2]); Hot water/AFA/H&E GL14570 (LS[2]); Hot-water/Bouin's/Mallory's GL14571 (LS[1]).

OTHER MATERIAL: same data as holotype, AFA/Hx GL14568 (W); Hot water/Bouin's/Mallory's GL14572 (LS[1]); Bouin's/H&E GL14573 (LS[2]); Hot water/AFA/H&E GL14574 (LS[2]); Bouin's/Mallory's GL14575 (LS[1]).

DESCRIPTION

External characteristics. Body about 1.2-2mm (mean=1.7mm) long, and about 0.5-0.9mm (mean=0.7mm) wide; oval or elliptical, dorso-ventrally compressed, but without flanges, or not dorso- ventrally compressed. Pigment creates impression of grey, actually a well defined pattern: dorsally a tracery extends from the base of the tentacles posteriorly and laterally to near the body margins, but becomes less dense towards the posterior. The pigment extends through the body outlining nerve tracts and major structures, and some is seen ventrally especially anterior to the mouth. Posterior adhesive disc pedunculate: disc diameter 280μm at rim, disc peduncle about 145μm in diameter. Epidermis syncitial with scattered nuclei, about 5-6μm high dorsally and ventrally. Cilia entirely absent.

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx inconspicuous. Pharynx directed antero-ventrally, as wide as long, about 180μm in diameter; strong, divided into anterior and posterior sphincter blocks by a region containing nucleated cells but few muscle fibres; lacking a non-cellular lip, with a conspicuous non-cellular lining (extending to buccal region), muscles not forming an obvious crenulate buccal rim. Pharynx sphincters slightly stronger posteriorly. Oesophagus inconspicuous. Gut darkly coloured, longer than wide to as wide as long; with ill-defined septa. Gastrodermis about 90μm high. Gut with diatoms.

Excretory system. Excretory pores lateral to mouth. Excretory ampulla a simple vacuole, thick

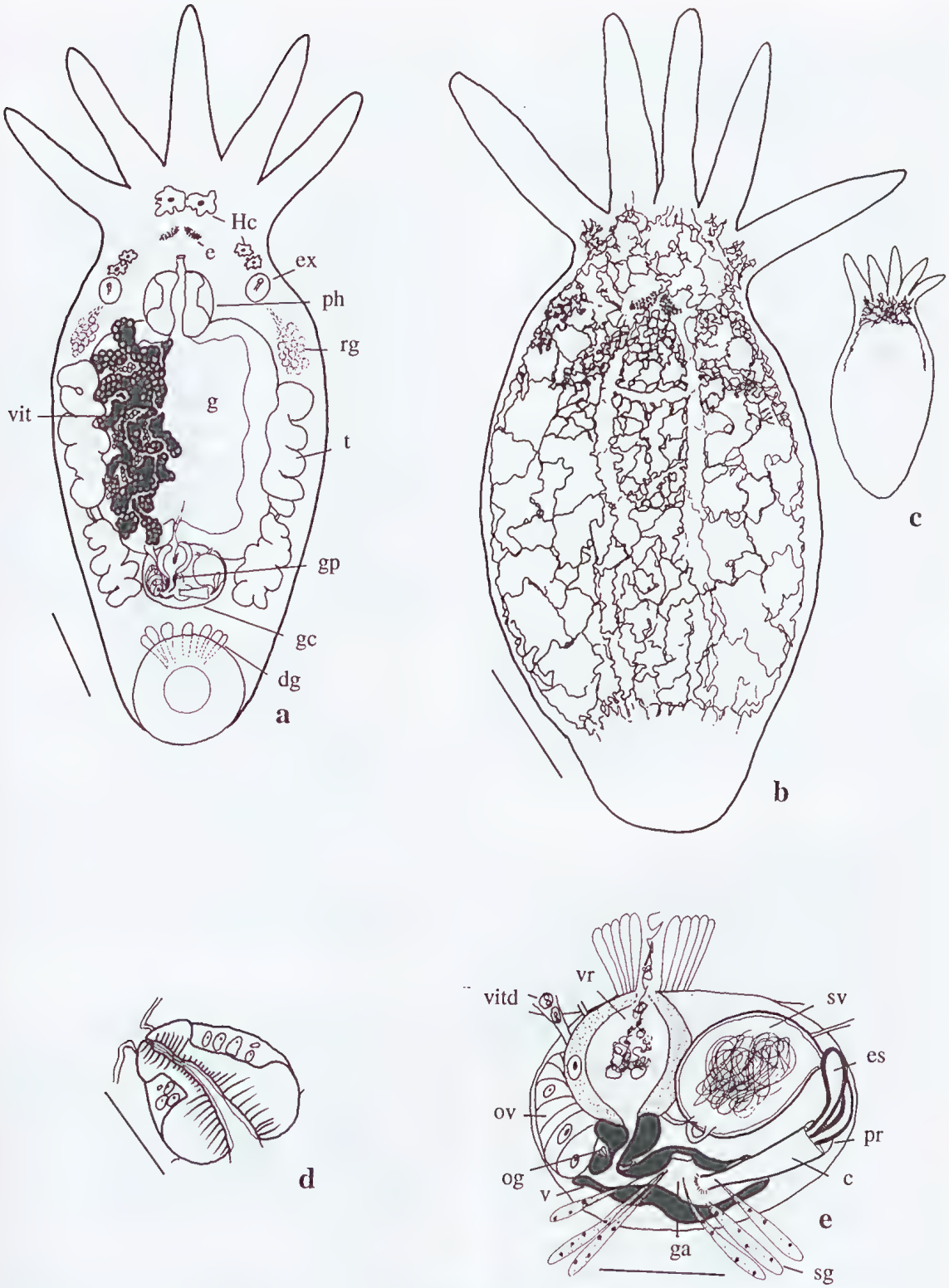


FIG. 1. *Temnocephala athertonensis* n.sp. a, internal anatomy of whole animal; b, dorsal pigment pattern; c, ventral pigment pattern; d, pharynx; e, detail of genital capsule. Scales: a,b, 250μm; c, not to scale; d,e, 100μm.

walled, about 75μm in diameter. Major excretory ducts conspicuous posterior to ampullae.

Nervous and sensory systems. Brain compact, transverse band. Major nerve trunks conspicuous in sections although pigment pattern outlines some. Eyes present, adjacent, with pigment mesh forming a single dark region, each about 40×25μm. Eye pigment granules irregular, mostly small (extremely fine), red-black.

Glands. Rhabdite glands in lateral fields anterior to anterior testes, numerous, 10 or more each side; each about 30μm across, with inconspicuous rhabdite tracts. Rhabdites only accumulate on tentacles. Haswell's cells conspicuous, six, a pair before brain, beside brain and before excretory pores (but median and lateral glands close together), each of the larger anterior pair irregular and about 50μm across, median pairs, smaller, about 30- 40μm across. Oesophageal glands inconspicuous (absent?). Ootype glands present (restricted to a small field). Shell glands present (a small group of eosinophilic glands posterior to gonopore). Posterio-lateral glands present, but difficult to see in whole mounts. Disc glands prominent, a discrete cluster.

Muscles. Longitudinal muscles of body wall of equal size or strength dorsally and ventrally. Circular muscles of body wall similar dorsally and ventrally. Dorso-ventral muscles weak. Attachment muscles of pharynx weak. Attachment muscles of adhesive disc moderately strong. Muscles controlling male organ strong immediately about the cirrus.

Reproductive system ♀. Gonopore mid-ventral, in posterior quarter of body. Genital atrium commodious. Genital complex contained in a connective tissue capsule. Ovary about 70μm in diameter. Vesicula resorbens present, about 80-100μm across, 15μm thick wall, with strong muscular duct or sphincter joining it to vagina; lying free of gut wall (in capsule), can open to gut. Seminal receptacles not present. Vagina strongly muscular, becoming less so proximally. Vitellaria dendritic, dorsal to ventral.

Reproductive system ♂. Testes elliptical: anterior about 170×230μm, lobulate, lateral to gut, posterior about 140×210μm, lobulate, lateral or posterior to gut. Vasa deferentia narrow, entering seminal vesicle separately. Seminal vesicle about 100μm in diameter. Ejaculatory sac present, with narrowed neck. Prostate bulb incorporated, i.e. continuation of cirrus base. Cirrus shaft gently curved. Cirrus hardly tapering, 80μm long, 35μm wide at base. Cirrus introvert not swollen, about 15μm or 1/6 length, only a weak collar of spinelets. Cirrus spinelets minute, few rows, i.e. <20.

ETYMOLOGY

The specific name pertains to the locality.

REMARKS

These worms from small freshwater crabs resemble most closely *T. minor* Haswell, 1888, the only species described with a grey tracery of pigment. The present species is only half the size of *T. minor* and the cirrus completely lacks the swollen introvert of that species. Furthermore, Haswell (1893) makes no mention of a capsule surrounding the genital organs, a characteristic of the present species. The pharynx of the present species is also distinctive. Posterio-lateral glands are present, but barely discernible. The only species described with such glands is *T. chaeropsis* Hett, 1925 from the crayfish '*Chaerops preissi*' (an old name: several species are now recognised from WA) from the region of Mammoth Cave, WA. In that species, however, the glands are conspicuous, adjacent and, furthermore, the worms lack conspicuous pigment except for the eyes (Hett, 1925).

Temnocephala butlerae n.sp.
(Figs 2,11d)

MATERIAL EXAMINED

HOLOTYPE: ex carapace *Holthuisana transversa* (Sundathelphusidae), Bore drain, Augathella (25.48°S, 146.35°E), 20 Apr. 1987, S. Butler, AFA/Haemalum GL14558 (W).

PARATYPES: same data as holotype, AFA/Hx GL14559 (W); Bouin's/H&E GL14560 (LS[3]).

OTHER MATERIAL: same data as holotype, AFA/H&E GL14561 (LS[1]).

DESCRIPTION

External characteristics. Body about 1.5mm long, and about 0.66mm wide; oval or elliptical, dorso-ventrally compressed, but without flanges. Pigment a light tracery over most of dorsal surface, extends to ventral surface (below eyes anterior to mouth). Posterior adhesive disc pedunculate: disc diameter 300μm at rim, disc peduncle 150μm in diameter. Epidermis syncitial, about 4μm high dorsally and ventrally. Cilia entirely absent.

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx conspicuous. Pharynx directed antero-ventrally, as wide as long, and about 160μm in diameter;

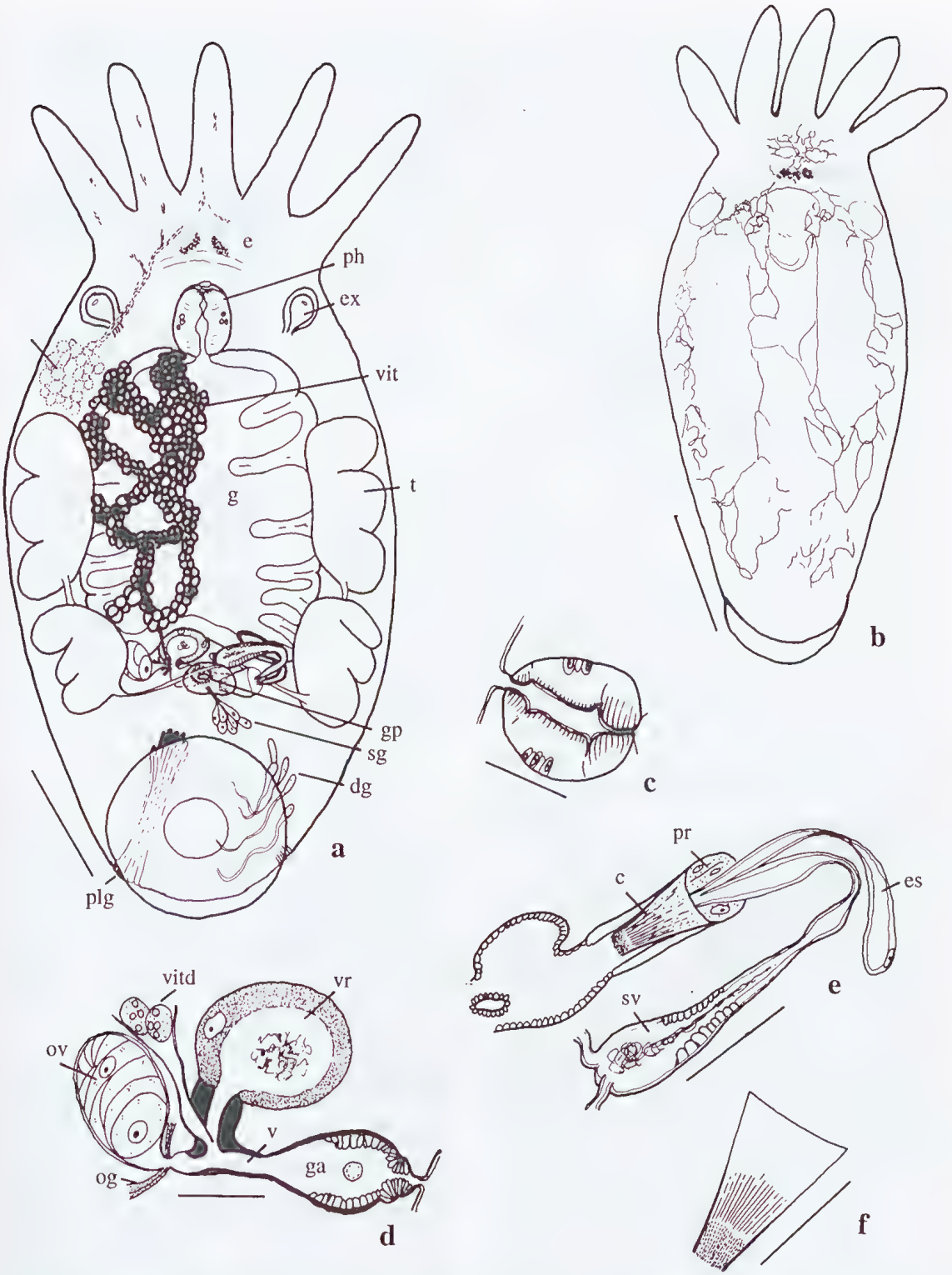


FIG. 2. *Temnocephala butlerae* n.sp. a, internal anatomy of whole animal; b, dorsal pigment pattern; c, pharynx; d, detail female reproductive system; e, detail male reproductive system; f, cirrus. Scales: a,b, 250μm; c-e, 100μm; f, 50μm.

strong, divided into anterior and posterior parts, containing nucleated cells within muscle blocks (concentrated between first and second blocks); lacking a non-cellular lip, with a conspicuous non-cellular lining, muscles forming a crenulate buccal rim. Pharynx sphincters stronger posteriorly. Oesophagus inconspicuous. Gut darkly coloured, longer than wide, weakly septate. Gastrodermis about 20-40μm high (numerous large cells filled with eosinophilic granules lie in gastrodermis).

Excretory system. Excretory pores posterior to mouth. Excretory ampulla a simple vacuole, thick walled (9- 10μm), about 90μm in diameter. Major excretory ducts inconspicuous.

Nervous and sensory systems. Brain compact, transverse band (20μm wide). Major nerve trunks inconspicuous. Eyes present, adjacent, with pigment mesh forming a single dark region, each about 35×25μm. Eye pigment granules irregular, mostly small, red-black.

Glands. Rhabdite glands in lateral fields anterior to anterior testes (well formed, resembling a bunch of grapes), numerous, 10 or more each side; each about 30μm in diameter, with prominent rhabdite tracts to tentacles. Rhabdites evident in ventral epidermis (anteriorly, as well as on tentacles). Two Haswell's cells outlined by pigment. Oesophageal glands prominent. Ootype glands present (not well developed). Shell glands present (eosinophilic, lying posterior to gonopore). Postero-lateral glands present (well developed, but hard to see as they are refractory to haematoxylin and eosin stains). Disc glands present (long tracks spread from peduncle/posterior body to discharge over the disc surface).

Muscles. Longitudinal muscles of body wall of equal size or strength dorsally and ventrally. Circular muscles of body wall similar dorsally and ventrally. Dorso-ventral muscles, attachment muscles of pharynx, of adhesive disc and those controlling male organ all weak.

Reproductive system ♀. Gonopore mid-ventral, in posterior third of body. Genital atrium commodious (sphincter present and muscular festoons about the walls). Genital complex scattered. Ovary about 80×50μm. Vesicula resorbens present, about 100×60μm, with 15μm thick wall, strong muscular duct or sphincter joining it to vagina; lying free of gut wall, not open to gut. Seminal receptacles not present. Vagina short, inner region weakly muscular, opening directly to atrium. Vitellaria dendritic, dorsal to ventral.

Reproductive system ♂. Testes elliptical: anterior about 270×200μm, lobulate, lateral to gut; posterior) about 230×210μm, lobulate, posterior or postero-lateral to gut. Vasa deferentia swollen, entering seminal vesicle separately. Seminal vesicle 95×55μm, with long reflexed ejaculatory duct from it to base of cirrus. Ejaculatory sac present (long), with narrowed neck. Prostate bulb incorporated, i.e. continuation of cirrus base. Cirrus shaft straight. Cirrus strongly tapering, about 70μm long, about 54μm wide at base. Cirrus introvert not swollen, weakly sclerotic, inner surface thrown in to fine ridges becoming a few rows of spinelets.

Etymology

The specific name refers to the collector, Dr Shirley Butler.

Remarks

As with *T. athertonensis* there is a tracery of pigment over the dorsal surface which resembles only one previously described species, *T. minor* Haswell, 1888. The nature of the cirrus and the presence of the postero-lateral glands separates it clearly from *T. minor*. It is close to *T. athertonensis*, but differs in having much finer pigment, a pharynx with a stronger central muscle region, a less muscular vagina, a small, broad cirrus, and most obviously in lacking the conspicuous capsule about the genital organs.

Temnocephala improcera n.sp.

(Figs 3,11e)

Material Examined

Holotype: ex *Caridina indistincta* (Atyidae), Murray R., nr Kirrama (18.01°S, 145.53°E), 26 Jul. 1984, L. Winsor, Form./H&E GL14576 (LS[2]).

Paratypes: same data as holotype, Form./Mallory's GL14577 (LS[1]).

Other Material: same data as holotype, Form./Hx GL14578 (damaged W).

Description

External characteristics. Body about 700μm long, and 350μm wide; oval or elliptical, not dorso-ventrally compressed. Pigment extends through body, prominent on dorsal and ventral surfaces. Posterior adhesive disc pedunculate: disc diameter 230μm at rim, disc peduncle about 100μm across. Epidermis syncitial, 3.5μm high dorsally, 5.5μm high ventrally. Cilia entirely absent.

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx

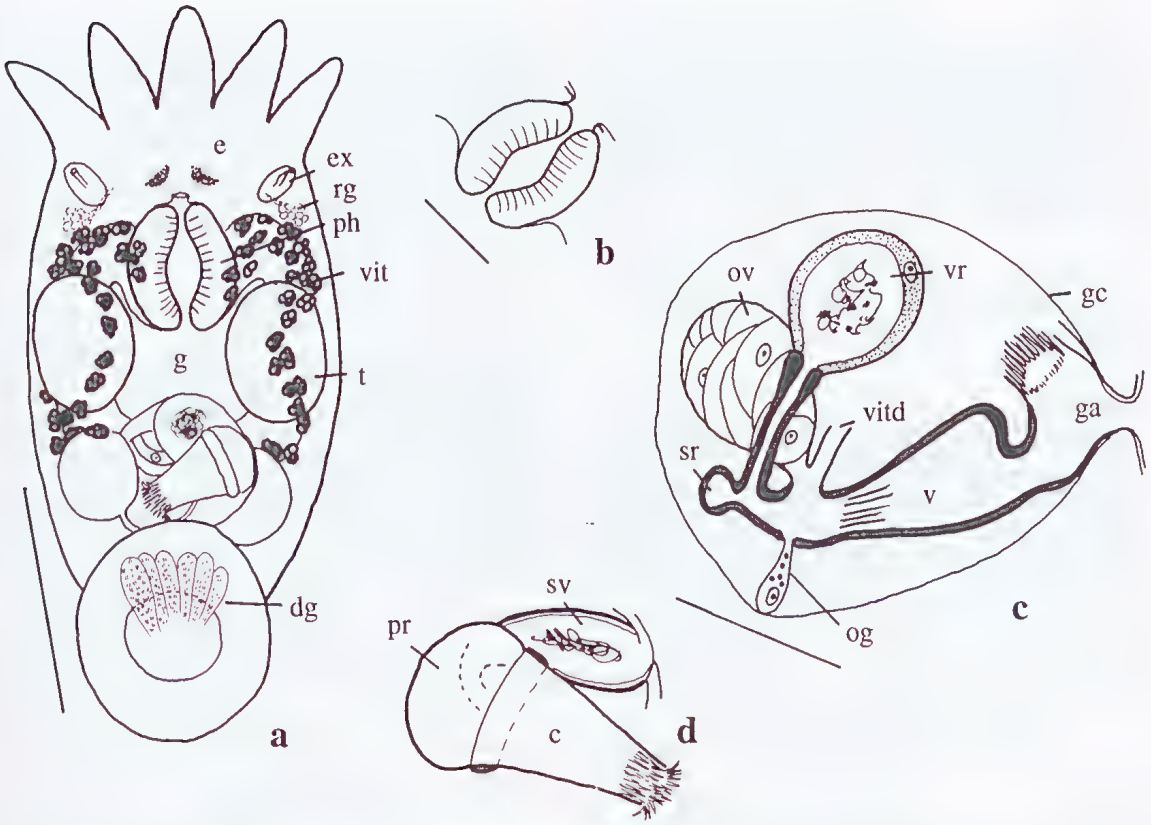


FIG. 3. *Temnocephala improcera* n.sp. a, internal anatomy of whole animal; b, pharynx; c, detail of female reproductive system; d, detail of male reproductive system. Scales: a, 250μm; b,c-d,100μm.

inconspicuous. Pharynx directed antero-ventrally, as wide as long, about 145×130μm; strong, undivided, with a few tiny eosinophilic glands in the muscle block; lacking a non- cellular lip, without a conspicuous non-cellular lining, muscles not forming an obvious crenulate buccal rim. Pharynx sphincters equal. Oesophagus inconspicuous. Gut darkly coloured (filled with brown globular (about 5-10μm) inclusions), longer than wide; with septa. Gastrodermis 60μm high.

Excretory system. Excretory pores anterior to mouth. Excretory ampulla a simple vacuole (but elongate), thick walled (12-14μm), about 70×30μm.

Nervous and sensory systems. Brain compact, transverse band. Major nerve trunks inconspicuous. Eyes present, discrete, well separated, about 20×30μm. Eye pigment granules irregular, mostly small, black-brown.

Glands. Rhabdite glands in lateral fields anterior to anterior testes. Rhabdites only accumulate on tentacles (?). Haswell's cells and oesophageal glands inconspicuous (absent?). Ootype glands present. Shell glands and postero-lateral glands absent. Disc glands conspicuous, filling the posterior body.

Muscles. Longitudinal muscles of body wall stronger ventrally. Circular muscles of body wall similar dorsally and ventrally. Dorso-ventral muscles weak. Attachment muscles of pharynx weak. Attachment muscles of adhesive disc strong. Muscles controlling male organ weak.

Reproductive system ♀. Gonopore mid-ventral, in posterior third of body. Genital atrium small. Genital complex contained in a connective tissue capsule. Ovary about 120×60μm. Vesicula resorbens present, about 70×35μm, 7μm thick wall; lying free of gut wall, not open to gut. Seminal receptacle single. Vaginal teeth absent. Vagina long, compartmentalised. Vitellaria scattered laterally, dorsal to ventral.

Reproductive system ♂. Testes rounded: anterior about 150μm in diameter, smooth, lateral to gut, posterior about 100μm in diameter, smooth, lateral or postero-lateral to gut. Vasa deferentia narrow, entering seminal vesicle separately. Seminal vesicle about 35×100μm. Ejaculatory

sac absent (?). Prostate bulb separate, i.e. wider than cirrus base. Cirrus shaft straight. Cirrus hardly tapering, 100μm long, 70μm wide at base, with basal collar. Cirrus introvert not swollen, about 25μm or 1/4 of the cirrus length. Cirrus spinelets moderately sized, filling inside, few rows, i.e. <20.

ETYMOLOGY

From *improcerus* L. = short, referring to the cirrus.

REMARKS

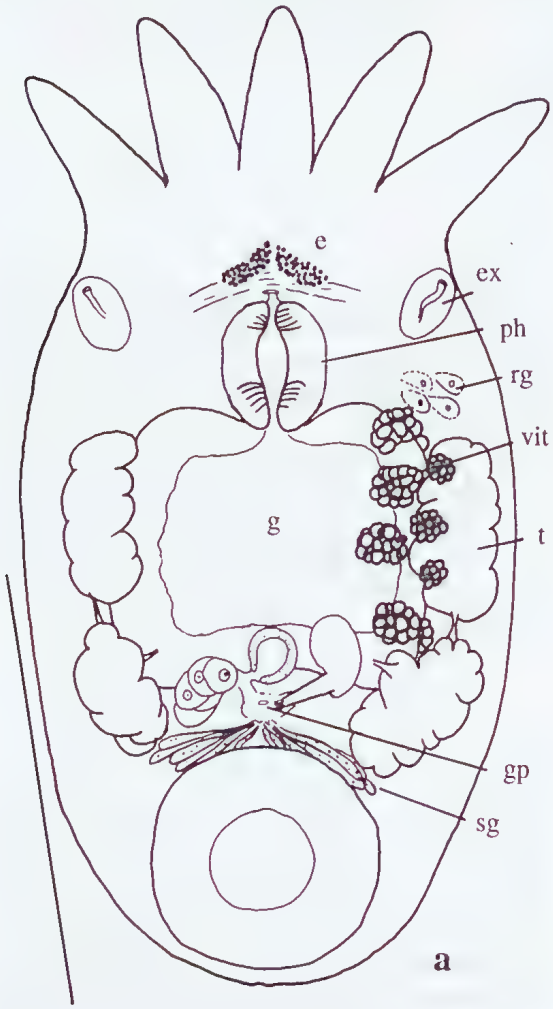
The combination of a pigmented body and the presence of a genital capsule means this species resembles most closely *T. athertonensis* (see above). However, it is much smaller, lacks the postero-lateral glands (though these are poorly developed in *T. athertonensis*), has smooth not lobulate testes, possesses a single seminal receptacle and has a short broad cirrus with a distinctive basal collar: none of these characters are shared with *T. athertonensis*.

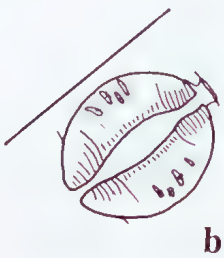
Temnocephala minuta n.sp.
(Fig. 4)

MATERIAL EXAMINED

HOLOTYPE: ex *Paratya australiensis* (Atyidae), Sandy Ck tributary of Dawson R. nr Taroom (25.39°S, 149.48°E), 3 Dec. 1986, L. Cannon & J. Jennings, AFA/Haemalum., GL14555 (W).

PARATYPE: same data as holotype, AFA/H&E GL14556 (LS[2]).





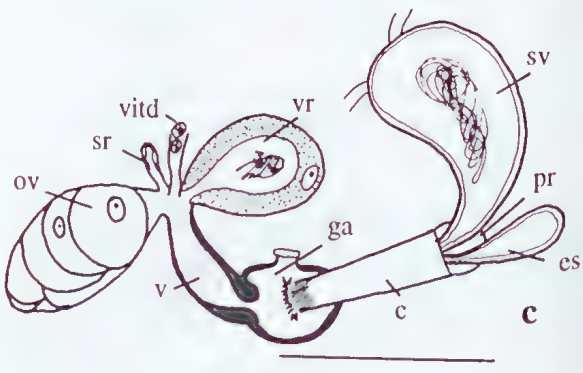


FIG. 4. *Temnocephala minuta* n.sp. a, internal anatomy of whole animal; b, pharynx; c, detail of reproductive systems. Scales: a, 250μm; b, 100μm; c, 50μm.

DESCRIPTION

External characteristics. Body about 550μm long, and 300μm wide; rounded to oval or elliptical, dorso-ventrally compressed, but without flanges. Pigment confined to eyes. Posterior adhesive disc pedunculate: disc diameter 120μm at rim, disc peduncle about 50μm in diameter. Epidermis syncitial, about 2μm high dorsally and ventrally. Cilia entirely absent.

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx inconspicuous. Pharynx directed antero-ventrally, as wide as long, about 80μm; strong, undivided, with nucleated cells in muscle blocks; lacking a non-cellular lip, without a conspicuous non-cellular lining, muscles not forming a crenulate buccal rim. Pharynx sphincters stronger posteriorly. Oesophagus inconspicuous. Gut lacking colour, as wide as long; without septa. Gastrodermis about 20-30μm high. Gut contains bacteria.

Excretory system. Excretory pores lateral to mouth. Excretory ampulla a simple vacuole, thick walled, about 30μm in diameter. Major excretory ducts inconspicuous.

Nervous and sensory systems. Brain compact, transverse band. Eyes present, contiguous, 25×15μm. Eye pigment granules irregular, mostly small, red-black.

Glands. Rhabdite glands in lateral fields anterior to anterior testes, few <10 each side; 12-15μm in diameter, with inconspicuous rhabdite tracts. Rhabdites apparently only accumulate on tentacles. Oesophageal glands and ootype glands inconspicuous (absent?). Shell glands present (a small cluster ventral to gonopore). Postero-lateral glands absent. Disc glands present.

Muscles. Longitudinal muscles of body wall stronger ventrally (especially at base of tentacles). Circular muscles of body wall similar dorsally and ventrally. Dorso-ventral muscles strong. Attachment muscles of pharynx weak. Attachment muscles of adhesive disc strong. Muscles controlling male organ weak.

Reproductive system ♀. Genital atrium small (but muscular). Genital complex scattered. Ovary about 30-50μm in diameter. Vesicula resorbens present, about 25-30μm across, 5μm thick wall; lying free of gut wall, not open to gut. Seminal receptacle, single, 7×3μm. Vagina short, simple (but with sphincter at opening to genital atrium). Vitellaria clustered, laterally above and below testes.

Reproductive system ♂. Testes elliptical: anterior about 110×66μm, lobulate, lateral to gut, posterior about 100×63μm, lobulate, posterior to gut. Vasa deferentia narrow. Seminal vesicle about 63×40μm. Ejaculatory sac present, with narrowed neck. Prostate bulb incorporated, i.e. continuation of cirrus base. Cirrus shaft straight. Cirrus hardly tapering, 36μm long, 11μm wide at base. Cirrus introvert not swollen, 7μm or 1/5 of the cirrus length. Cirrus spinelets minute, few rows, i.e. <20.

ETYMOLOGY

From *minutus* L. = small, refers to body size.

REMARKS

This species resembles most closely *T. cita* Hickman, 1967 in lacking pigment except for the eyes and in possession of a cirrus without a median spine. *T. cita* is very much larger, has a cirrus about 5× as big, 4 seminal receptacles (not one), and smooth, unequal testes (not subequal, lobed ones). The only other unpigmented species are *T. dendyi* Haswell, 1893 and *T. engaei* Haswell, 1893. Both these species have a median spine within the cirrus.

Temnocephala neqae n.sp.
(Figs 5,11f)

MATERIAL EXAMINED

HOLOTYPE: ex gills of *Macrobrachium rosenbergii* (Palaemonidae), Mitchell R. at Mt Carbine (16.32°S,145.08°E), Nov. 1981, J. Short, Form./Hx., GL14518 (W).

PARATYPES: same data as holotype, GL14519 (W); ex gills of *M. rosenbergii* (Palaemonidae), Mitchell R., Dec. 1981, B. Power, Form./Mallory's GL14525-6 (LS[2,3]); Form./Gomori's GL14527 (TS[2]).

OTHER MATERIAL: same data as holotype, GL14520-35 (W); Form./H&E GL14537 (LS[3]); GL14538 (egg on gills of host); ex gills of *M. rosenbergii* (Palaemonidae), Mitchell R., Dec. 1981, B. Power, Form./Mallory's GL14536 (W).

DESCRIPTION

External characteristics. Body about 800-1400μm (mean=1040μm) long, and 430-720μm (mean=540μm) wide; oval or elliptical, dorso-ventrally compressed, with flanged edges. Pigment confined to eyes. Posterior adhesive disc pedunculate: disc diameter 220μm at rim, disc peduncle about 125μm across. Epidermis syncitial, 5μm high dorsally, 3μm high ventrally. Cilia entirely absent.

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx inconspicuous. Pharynx directed ventrally, wider

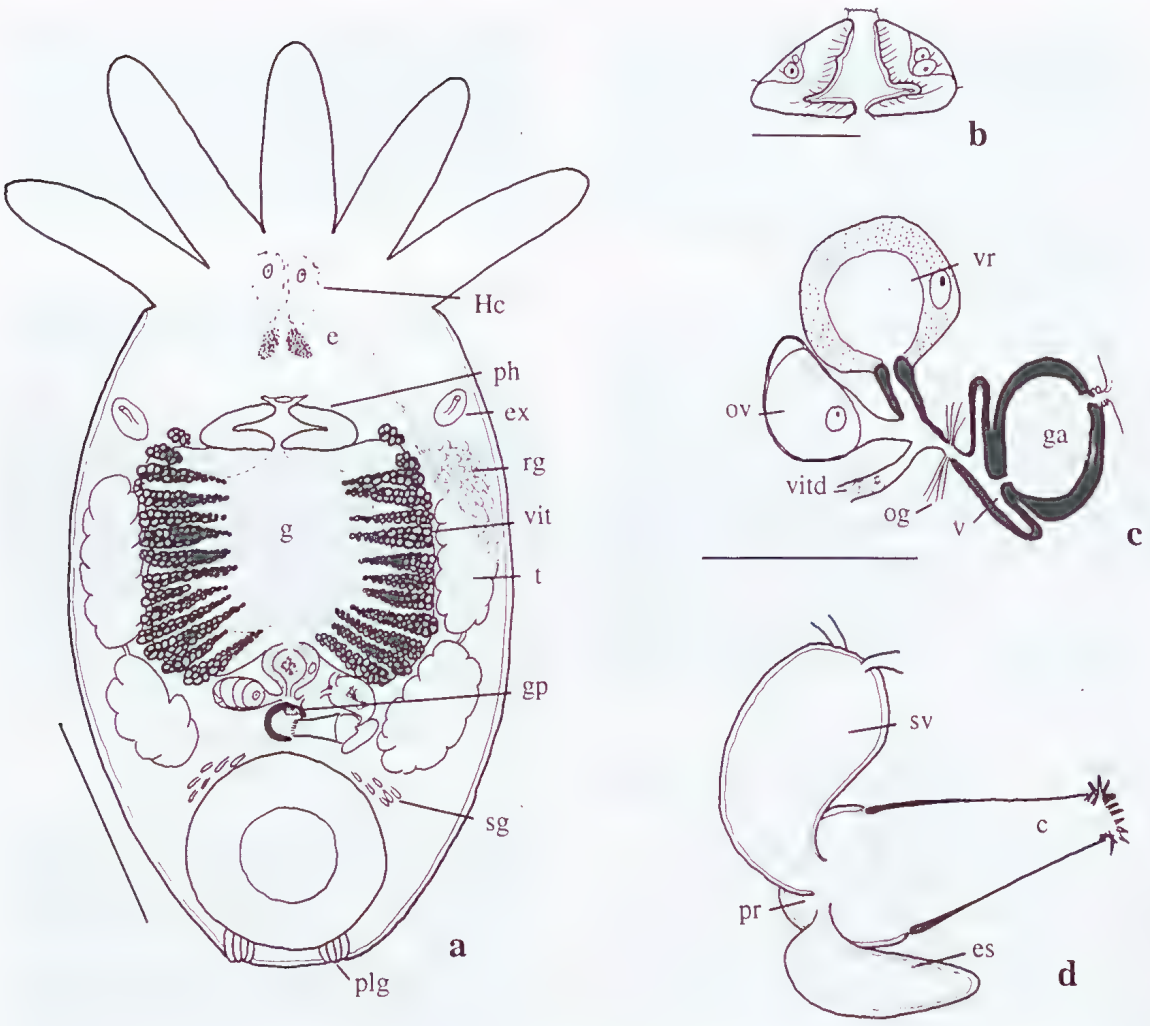


FIG. 5. *Temnocephala neqae* n.sp. a, internal anatomy of whole animal; b, pharynx; c, detail of female reproductive system; d, detail of male reproductive system. Scales: a, 250μm; b, 100μm; c-d, 50μm.

than long, about 95×180μm; strong, undivided, with nucleated cells within muscle blocks; lacking a non-cellular lip, with a conspicuous non-cellular lining, muscles forming a crenulate buccal rim. Pharynx sphincters stronger posteriorly. Oesophagus inconspicuous. Gut lacking colour, as wide as long; without septa. Gastrodermis to 16μm high. Gut contains ?rotifers.

Excretory system. Excretory pores posterior to mouth. Excretory ampulla a simple vacuole, thick walled (12μm), about 50×36μm. Major excretory ducts conspicuous.

Nervous and sensory systems. Brain compact, transverse band. Major nerve trunks inconspicuous. Eyes present, contiguous, about 40×30μm. Eye pigment granules irregular, mostly small, black-brown.

Glands. Rhabdite glands in lateral fields anterior to anterior testes, numerous, 10 or more each side; about 20μm in diameter, with prominent rhabdite tracts to tentacles. Rhabdites only accumulate on tentacles (?). Haswell's cells inconspicuous (only two before brain), each ill defined about 80×50μm. Oesophageal glands present. Ootype glands prominent. Shell glands in prominent lateral fields discharging to gonopore. Postero-lateral glands prominent. Disc glands present.

Muscles. Longitudinal muscles of body wall stronger ventrally. Circular muscles of body wall similar dorsally and ventrally. Dorso-ventral muscles and attachment muscles of pharynx weak. Attachment muscles of adhesive disc mod-

erately strong. Muscles controlling male organ strong.

Reproductive system ♀. Gonopore mid-ventral, in posterior third of body. Genital atrium large, muscular. Genital complex scattered. Ovary about 62×50μm. Vesicula resorbens present, about 48×80μm, 13μm thick wall; embedded in gut wall, opens to gut (in some). Seminal receptacles not present. Vaginal teeth absent. Vagina simple (muscular). Vitellaria dendritic, lateral. Egg capsules ellipsoid, about 300×100μm; attached on end on a stalk, on gills.

Reproductive system ♂. Testes elliptical: anterior about 170×85μm, lobulate, lateral to gut; posterior about 165×95μm, lobulate, lateral to or posterior to gut. Vasa deferentia narrow, entering seminal vesicle separately. Seminal vesicle about 70×30μm. Ejaculatory sac present, with narrowed neck. Prostate bulb separate, i.e. wider than cirrus base. Cirrus shaft straight. Cirrus hardly tapering, 52μm long, 30μm wide at base. Cirrus introvert not swollen, only about 12μm or 1/4 of the cirrus length, i.e. about the length of the 2-3 rows of cirral spines. Cirrus spinelets moderately sized, few rows, i.e. <20.

Etymology

The specific name refers to northeast Queensland.

Remarks

The only described species with prominent postero-lateral glands is *Temnocephala chaeropsis* Hett, 1925 from a crayfish '*Chaerops preissi*' from near Mammoth Cave, WA. Unlike the present species, the glands are very close together; among other differences *T. chaeropsis* is much bigger, has four seminal receptacles, evidently lacks an ejaculatory sac and the introvert of the cirrus is more elaborate. Both *T. athertonensis* and *T. butlerae* (see above) also have postero-lateral glands; in neither species are they prominent and easily seen; furthermore, both species are pigmented, unlike the present species.

Temnocephala queenslandensis n.sp.
(Fig. 6)

Material Examined

Holotype: ex *Macrobrachium australiense* (Palaemonidae), Hayes Ck off Moggill Ck Brisbane (27.30.4°S, 152.55.8°E), 7 Mar. 1990, L. Cannon & K. Sewell, AFA/Haemalum GL14539 (W).

Paratypes: same data as holotype, AFA/ H&E GL14540-1 (LS[1,1]).

Other Material: ex *M. australiense* (Palaemonidae), Highvale (27.23°S, 152.48°E), 10 May 1990, L. Cannon & K. Sewell, Bouin's/H&E GL14542 (LS[1]); AFA/Haemalum GL14543 (W); Upper Cedar Ck (27.19.2°S, 152.55.8°E), 10 Apr. 1990, L. Cannon & K. Sewell, Boiling water/AFA/Haemalum GL14544 (W); same data as holotype 14545-9 (W); Ithaca Ck, Brisbane (27.29°S, 152.57°E), 20 Oct. 1988, J. Short, Form./Hx GL14550 (W); Gold Ck, Brisbane (27.25.6°S, 152.50.9°E), 6 Mar. 1990, L. Cannon & K. Sewell, AFA/Haemalum G14551-2 (W); Bouin's/H&E G14553-4 (FS[1,1]); Booloumba Ck (26.39°S, 152.39°E), 23 Mar. 1990, L. Cannon & K. Sewell, AFA/Haemalum G14609-11 (W); AFA/H&E G14612-5 (LS[1,1,1,1,]); Six mile Ck, Cooran (26.20°S, 152.50°E), 23 Mar. 1990, L. Cannon & K. Sewell, SUSA/Haemalum GL14616 (W); SUSA/Haemalum GL14617-8 (LS[1,1]); AFA/Haemalum GL14619-21 (W); Bouin's/H&E GL14622-3 (W); Kin Kin Ck (26.16°S, 152.53°E), 23 Mar. 1990, L. Cannon & K. Sewell, Bouin's/Haemalum GL14624-5 (W); AFA/Haemalum GL14626-28 (W); AFA/H&E GL14629-30 (LS[2,1]); Bouin's/H&E GL14631 (LS[2]); Kroombit Ck, Kroombit Tops (24.23.0°S, 151.00.2°E), 20 Sep. 1990, L. Cannon & K. Sewell, AFA/Hx GL14632 (W); AFA/H&E GL14633 (LS[1]); Tributary of Broken R., Eungella NP (28.10.8°S, 148.32.2°E), 21 Sep. 1990, L. Cannon & K. Sewell, Hot water/AFA/Hx GL14634-5 (W); Bouin's/H&E GL14636-8 (LS[1,1,1]); Stuart Ck, Townsville (19.19.4°S, 146.50.2°E), 23 Sep. 1990, L. Cannon & K. Sewell, AFA/Hx GL14639 (W); Bouin's/H&E GL14640 (LS[1]); upper Pozzle Ck, Hidden Valley, Paluma (18.59°S, 146.01°E), 2 May 1982, L. Winsor, Form./Hx GL14641 (W); Form./H&E GL14642-3 (LS[2,1]); tributary (No. 4) of Blackfellow Ck, Edmonton (17.00.6 E, 145.43.0°E), 28 Sep. 1990, L. Cannon & K. Sewell, AFA/Hx GL14646 (W); Rocky Ck, Carbeen (17.11.2°S, 145.26.8°E), 28 Sep. 1990, L. Cannon & K. Sewell, Bouin's/H&E GL14647-8 (LS[1,1]); Jumrun Ck, Kuranda (16.46.8°S, 145.38.0°E), 28 Sep. 1990, L. Cannon & K. Sewell, Hot water/AFA/Hx GL14649; Bouin's/H&E GL14650,18241 (LS[1,2]); Western R., Cragg Family Bridge, Winton (22.25.0°S, 143.01.9°E), 2 Oct. 1990, L. Cannon & K. Sewell, AFA/Hx GL18242 (W); Bouin's/H&E GL18243 (LS[1]); Longreach Waterhole, Longreach (23.24.7°S, 144.13.8°E), 3 Oct. 1990, L. Cannon & K. Sewell, Bouin's/H&E GL18244-5 (LS[2,1]); Lagoon Ck, Barcaldine (23.33.5°S, 145.16.6°E), 23 Sep. 1990, S. Cook, Alcohol/Haemalum GL18246-48 (W); Dawson R., Taroom (25.39°S, 149.48°E), 3 Dec. 1986, L. Cannon & J. Jennings, AFA/Haemalum GL18249-50 (W); AFA/H&E GL18251 (LS[2]); Carnarvon Ck (25.06.5°S, 148.18.3°E), 18 Sep. 1990, S. Cook, Alcohol/Hx GL18252 (W); ex *M. tolmerum* (Palaemoni-

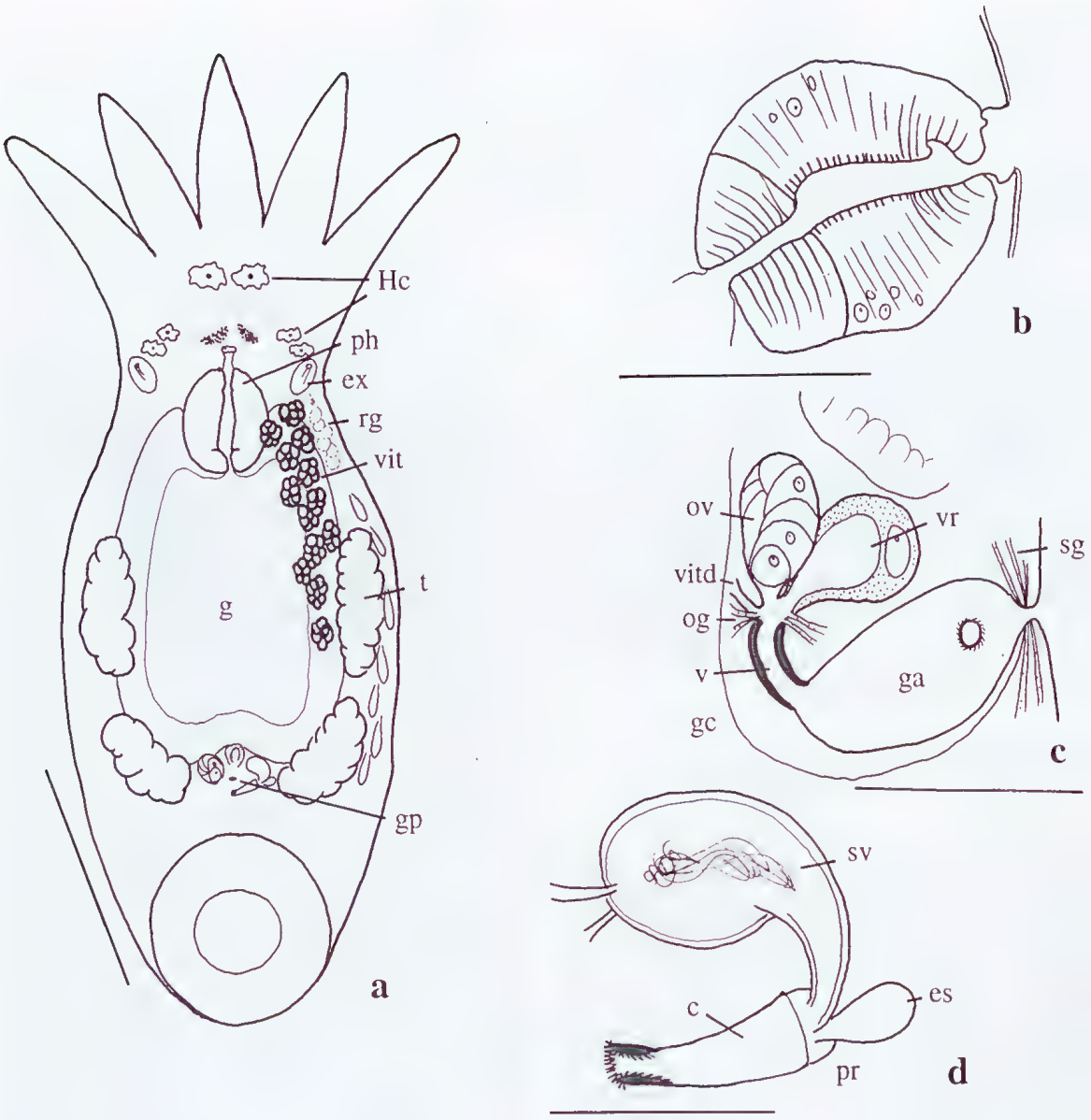


FIG. 6. *Temnocephala queenslandensis* n.sp. a, internal anatomy of whole animal; b, pharynx; c, detail of female reproductive system; d, detail of male reproductive system. Scales: a 250μm; c, 100μm; b, d, 50μm.

dae), Freshwater Ck, Cairns (16.54.1°S, 145.42.4°E), 23 Sep. 1990, L. Cannon & K. Sewell, AFA/Hx GL14644 (W); Bouin's/H&E GL14645 (LS[1]).

DESCRIPTION

External characteristics. Body about 650-950μm (mean=775μm) long, and 290- 350μm (mean=315μm) wide; oval or elliptical, not dorso-ventrally compressed. Pigment confined to eyes. Posterior adhesive disc pedunculate: disc diameter 155μm at rim, disc peduncle about 70μm across. Epidermis syncitial (a strongly staining basement membrane and numerous cell walls seen), 2μm high dorsally and ventrally. Cilia entirely absent.

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx conspicuous. Pharynx directed antero-ventrally, as wide as long, about 80μm in diameter; strong, not divided into anterior and posterior parts, without conspicuous nucleate cells within muscle blocks; lacking a non-cellular lip, with a conspicuous non-cellular lining, muscles not forming an obvious crenulate buccal rim. Pharynx sphinc-

ters stronger posteriorly. Oesophagus inconspicuous. Gut lacking colour, as wide as long; without septa. Gastrodermis 50μm high.

Excretory system. Excretory pores lateral to mouth. Excretory ampulla a simple vacuole, thick walled (10μm), about 40×20μm. Major excretory ducts inconspicuous.

Nervous and sensory systems. Brain compact, transverse band. Major nerve trunks inconspicuous. Eyes present, contiguous, about 20×10μm. Eye pigment granules medium, even sized, black-brown.

Glands. Rhabdite glands extending laterally beyond testes, numerous, 10 or more each side; 7-10μm in diameter, with prominent rhabdite tracts to tentacles. Rhabdites only accumulate on tentacles. Haswell's cells present, 2 before eyes and two before each excretory ampulla. Oesophageal glands present. Ootype glands present. Shell glands in prominent lateral fields discharging to gonopore. Postero-lateral glands inconspicuous (absent?). Disc glands present.

Muscles. Longitudinal muscles of body wall of equal size or strength dorsally and ventrally. Circular muscles of body wall similar dorsally and ventrally. Dorso-ventral muscles moderately strong. Attachment muscles of pharynx weak. Attachment muscles of adhesive disc strong (moderately). Muscles controlling male organ weak.

Reproductive system ♀. Gonopore mid-ventral, in posterior third of body. Genital atrium commodious. Genital complex in weak capsule. Ovary about 115×40μm. Vesicula resorbens present, about 40μm in diameter, 8-10μm thick wall; embedded in gut wall, opens to gut (in some). Seminal receptacles absent. Vagina short, simple. Vitellaria in lateral clusters.

Reproductive system ♂. Testes elliptical: anterior about 115×40μm, lobulate, lateral to gut; posterior about 100×50μm, lobulate, posterior to gut. Vasa deferentia swollen, entering seminal vesicle separately. Seminal vesicle about 50×20μm. Ejaculatory sac present, but small with narrowed neck. Prostate bulb incorporated, i.e. continuation of cirrus base (not well defined). Cirrus shaft gently curved (proximally very fine). Cirrus hardly tapering, 45μm long, 17μm wide at base. Cirrus introvert not swollen (slightly thickened and noticeably more thickened than shaft), about 9μm or nearly 1/5 of the cirrus length. Cirrus spinelets moderately sized, few rows, i.e. <20.

ETYMOLOGY

The specific name refers to the locality, Queensland.

REMARKS

Four species completely lack pigment except for the eyes, viz., *T. cita* Hickman, 1967, *T. dendyi* Haswell, 1893 *T. engaei* Haswell, 1893 and *T. minuta* (see above). Only *T. cita* and *T. minuta* have a cirrus without a median spine, but the cirrus is much larger (3-4×) in *T. cita*, and is slightly smaller and straighter in *T. minuta*, than in the present species. *T. cita* also has smooth, oval testes of unequal size and possesses 4 seminal receptacles, whereas *T. minuta* has a single seminal receptacle. These characters distinguish these worms from *T. queenslandensis*.

Temnocephala sp.

MATERIAL EXAMINED

ex shrimp (Atyidae), Sandy Ck nr Taroom (25.39°S, 149.48°E), 3 Dec. 1986, L. Cannon & J. Jennings, Form./Haemalum., GL14517 (W).

DESCRIPTION

External characteristics. Body about 315μm long, and 200μm wide; rounded, dorso-ventrally compressed, but without flanges. Pigment entirely absent, i.e. not even eyes. Posterior adhesive disc pedunculate: disc diameter 100μm at rim, disc peduncle about 60μm across. Epidermis syncitial (?). Cilia entirely absent.

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx inconspicuous. Pharynx directed antero-ventrally, wider than long, about 56×42μm; strong, undivided, without prominent nucleate cells in muscle blocks; lacking a non-cellular lip, without a conspicuous non-cellular lining, muscles forming a slightly crenulate buccal rim. Pharynx sphincters stronger posteriorly. Oesophagus inconspicuous. Gut lacking colour, as wide as long; without septa.

Excretory system. Excretory pores dorso-lateral, lateral to mouth. Excretory ampullae about 40×35μm, thick walled (about 5μm). Major excretory ducts inconspicuous.

Nervous and sensory systems. Brain bilobed. Major nerve trunks inconspicuous. Eyes absent.

Glands. Rhabdite glands lateral to testes; with inconspicuous rhabdite tracts.

Muscles. Longitudinal muscles of body wall of equal size or strength dorsally and ventrally.

Reproductive system ♀. Gonopore mid-ven-

tral, in posterior third of body. Genital atrium small (but muscular). Genital complex scattered. Ovary about 18×10μm. Vesicula resorbens present, about 31×21μm; lying free of gut wall. Seminal receptacles not present (?). Vagina short, simple. Vitellaria dendritic.

Reproductive system ♂. Testes elliptical: anterior about 70×35μm, lobulate, lateral to gut, posterior about 35×40μm, lobulate, posterior to gut. Vasa deferentia swollen. Seminal vesicle about 35×18μm. Ejaculatory sac present. Cirrus shaft gently curved. Cirrus hardly tapering, 36μm long, 14μm wide at base. Cirrus introvert not swollen, about 9μm or 1/4 of the cirrus length. Cirrus spinelets minute, few rows, i.e. <20.

REMARKS

As this is a single immature specimen no type designation is made. The complete lack of eyes, however, strongly suggests this will prove a new species.

Temnohaswellia Pereira & Cuocolo, 1941

Generic diagnosis. Temnocephalidae with 6 anterior tentacles, a posterior adhesive disc, two pairs of testes postero-lateral to gut.

Temnohaswellia pugna n.sp.
(Figs 7,11g)

MATERIAL EXAMINED

HOLOTYPE: ex *Caridina* sp. (*?nilotica*) (Atyidae), Aplin Weir on Ross R., Townsville (19.22°S, 146.44°E), 1976, L. Winsor, Form./Picrocarmine GL14579 (W).

DESCRIPTION

External characteristics. Body about 1700μm long (tentacles about 500μm), and 1000μm wide; rounded, dorso-ventrally compressed, with flanged edges. Pigment confined to eyes and adjacent area (just a scatter between eyes). Posterior adhesive disc pedunculate: disc diameter 350μm at rim, disc peduncle about 180μm across. Disc musculature does not create surface ridges. Epidermis syncitial (?). Cilia entirely absent.

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx inconspicuous. Pharynx directed antero-ven-

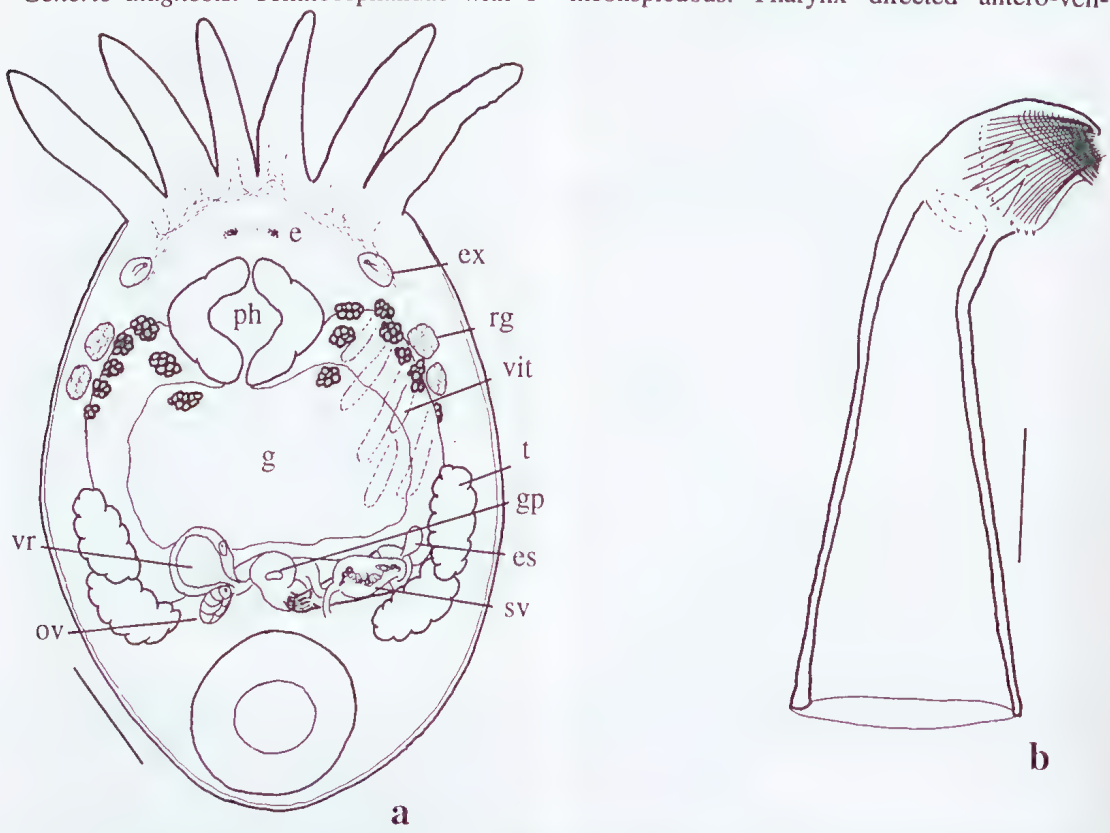


FIG. 7. *Temnohaswellia pugna* n.sp. a, internal anatomy of whole animal; b, cirrus. Scales: a, 250μm; b, 50μm.

trally, wider than long, about 360×270μm; strong, undivided, with nucleate cells within muscle blocks; lacking a non-cellular lip, without a conspicuous non-cellular lining, muscles forming a crenulate buccal rim. Pharynx sphincters subequal, slightly stronger posteriorly. Oesophagus inconspicuous. Gut lacking colour, with 3 ill-defined septa per side. Gastrodermis about 80μm high. Gut contains muscle, crustacea and diatoms.

Excretory system. Excretory pores lateral to mouth. Excretory ampulla strongly coiled, thin walled (10μm), about 90×70μm. Major excretory ducts inconspicuous.

Nervous and sensory systems. Brain compact, transverse band. Major nerve trunks inconspicuous. Eyes present, discrete, well separated (but scattered granules between them), about 20μm across. Eye pigment granules irregular, mostly small, black-brown.

Glands. Rhabdite glands? in lateral fields anterior to anterior testes, in two clumps (the smaller is posterior), with prominent rhabdite tracts to tentacles. Rhabdites evident in dorsal and ventral epidermis. Haswell's cells inconspicuous (absent?). Postero-lateral glands absent.

Reproductive system ♀. Gonopore mid-ventral, in posterior third of body. Genital atrium small. Genital complex scattered. Ovary about 70×5μm. Vesicula resorbens present, about 140μm across, 15μm thick wall; lying free of gut wall, not open to gut. Seminal receptacles absent (?). It is not clear from the specimen if vaginal teeth or muscular ribs are present. Vagina complex, outer region muscular, inner simpler. Vitellaria dendritic, dorsal over gut and lateral (plus some ventral behind pharynx).

Reproductive system ♂. Testes elliptical: anterior about 250×100μm, posterior about 220×100μm, lobulate, slightly overlapping. Vasa deferentia swollen. Seminal vesicle sinuous about same length as cirrus. Ejaculatory sac present, with narrowed neck. Prostate bulb incorporated, i.e. continuation of cirrus base. Cirrus shaft straight. Cirrus strongly tapering, 240μm long, 90μm wide at base. Cirrus introvert swollen, slightly thickened and reflexed as with a clenched fist, about 80×45μm or 1/3 of the cirrus length. Cirrus spines apparently at base of introvert. Cirrus spinelets minute to moderately sized, numerous rows, i.e. >20.

ETYMOLOGY

From *pugnus* L. = fist, referring to the shape of the cirrus introvert.

REMARKS

Pereira & Cuocolo (1941) erected the genus *Temnohaswellia* with *T. novaezealandiae* (Haswell, 1888) as the type species. They included in the genus *T. comes* (Haswell, 1893) and placed the poorly described *T. simulator* (Haswell, 1924) in synonymy with it. Baer (1953) rejected the genus believing the possession of 6 tentacles insufficient justification on which to erect a new genus, although he allowed that coupled with the vaginal teeth found in *T. novaezealandiae* there may be justification. This latter character is, however, absent from *T. comes*.

First, Haswell (1924) who was a careful worker clearly distinguished *T. simulator* from *T. comes*: *T. simulator* is here recognised as a valid species. Secondly, Haswell (on the same page) suggests the elaborate vagina of *T. novaezealandiae* may be 'an enormous extension of the thick sphincter of *T. comes* and the metraterm which subtends it.' Thus Haswell clearly saw a link between these species. Further, the relatively posterior position of the testes (overlapping and at the rear of the gut) and the presence of two pairs of clumped glands at the anterior lateral margin of the gut as Fyfe (1942) showed in *T. novaezealandiae* I believe provide characters coupled with the others to indicate these species are related. Fyfe (1942) claimed these paired anterior glands were prostate glands: their position certainly is in more keeping with rhabdite glands. The material available is not adequate to distinguish this character, and regrettably Haswell (1893) did not fully describe *T. comes*. Nevertheless, I believe the genus *Temnohaswellia* Pereira & Cuocolo, 1941 should be recognised as valid. Of the three known species, viz. *T. comes* (Haswell, 1893) which is unpigmented, and T. simulator (Haswell, 1924) and *T. novaezealandiae* (Haswell, 1888) which are pigmented, the present species more closely resembles *T. comes*, but may be distinguished by the cirrus which, though possessing a distinctive introvert, is not curved as in *T. comes*.

Temnohaswellia tetrica n.sp.
(Fig. 8)

MATERIAL EXAMINED

HOLOTYPE: ex *Caridina* sp. (*?nilotica*) (Atyidae), Aplin Weir on Ross R., Townsville (19.22°S, 146.44°E), 1976, L. Winsor, Form./Picrocarmine GL14580 (W).

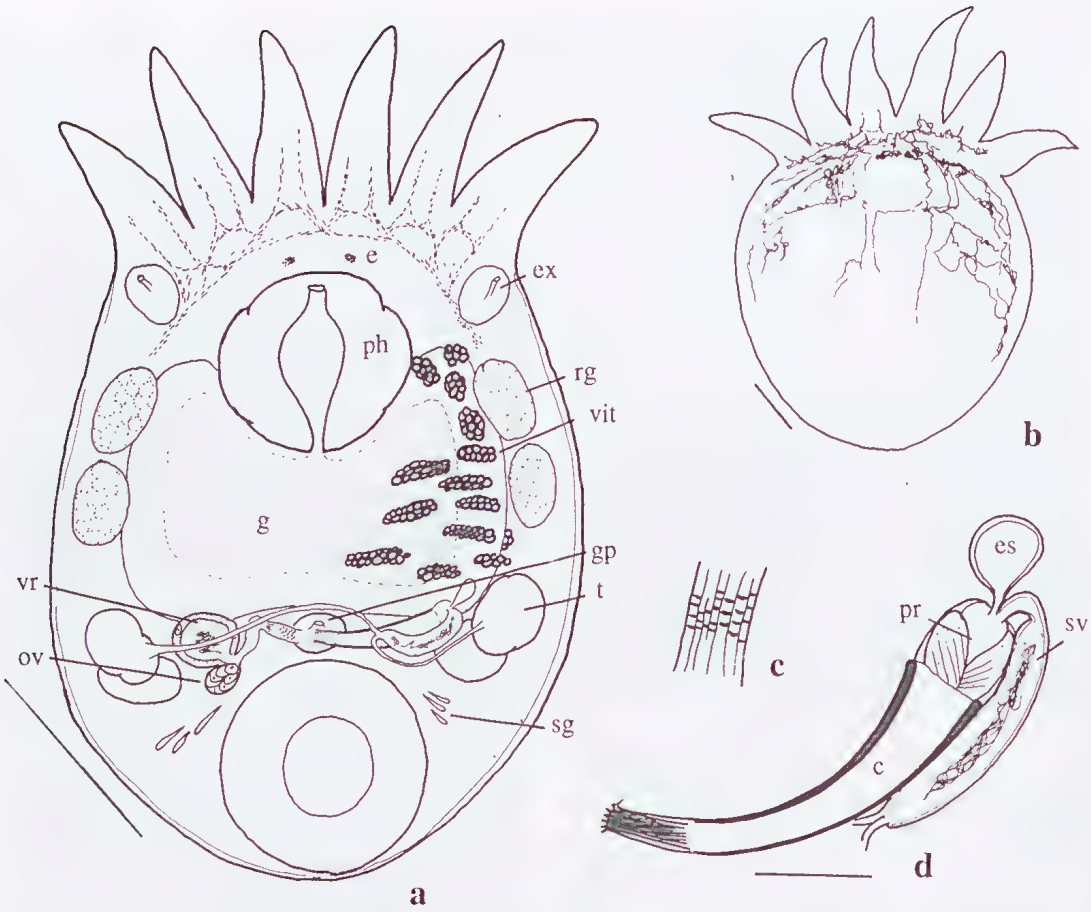


FIG. 8. *Temnohaswellia tetrica* n.sp. a, internal anatomy of whole animal; b, dorsal pigment pattern; c, detail of vaginal teeth; d, detail of male reproductive system. Scales: a,b, 250μm; c, not to scale; d, 100μm.

DESCRIPTION

External characteristics. Body about 2mm long (tentacles about 500μm), and 13mm wide; rounded, dorso-ventrally compressed, with flanged edges. Pigment a tracery over most of anterior dorsal surface. Posterior adhesive disc pedunculate: disc diameter 500μm at rim, disc peduncle about 250μm across. Epidermis syncitial (?). Cilia entirely absent (?).

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx conspicuous. Pharynx directed antero-ventrally, as wide as long, about 485μm across; strong, undivided, with nucleate cells within muscle blocks (?); lacking a non-cellular lip, without a conspicuous non-cellular lining, muscles forming a crenulate buccal rim. Pharynx sphincters equal (?). Oesophagus inconspicuous. Gut lacking colour, wider than long; without septa. Gut contains diatoms.

Excretory system. Excretory pores anterior to mouth. Excretory ampulla a simple vacuole, thick walled, about 180μm in diameter. Major excretory ducts inconspicuous.

Nervous and sensory systems. Eyes adjacent, about 30μm across, linked with a pigment mesh forming a single dark region. Eye pigment granules irregular, mostly small, black-brown.

Glands. Rhabdite glands? in lateral fields anterior to anterior testes (in two tandem clumps), individual gland cells within these clumps are not readily distinguishable; clumps 140-170 × 120 μm. With prominent rhabdite tracts to tentacles; rhabdites only accumulate on tentacles (?). Haswell's cells, oesophageal glands and ootype glands inconspicuous (absent?). Shell glands in

prominent lateral fields. Postero-lateral glands absent.

Reproductive system ♀. Gonopore mid-ventral, in posterior third of body. Genital atrium small. Genital complex scattered. Ovary about 80μm in diameter. Vesicula resorbens present, about 120μm across; lying free of gut wall, not open to gut. Seminal receptacles absent (?). Vaginal teeth present, about 5 or 6 rows of fine scale-like teeth in columns. Vagina long, compartmentalised. Vitellaria dendritic, dorsal to ventral.

Reproductive system ♂. Testes rounded, smooth, about 175μm in diameter, both posterior to the gut and slightly overlapping one another (the posterior more dorsal pair vacuolated and apparently invaded by nematodes). Vasa deferentia narrow (?), entering seminal vesicle separately. Seminal vesicle about 35×200μm. Ejaculatory sac present, with narrowed neck. Prostate bulb incorporated, i.e. continuation of cirrus base. Cirrus shaft curved. Cirrus hardly tapering, 350μm long, 70μm wide at base. Cirrus introvert not swollen, about 70μm or 1/5 of the cirrus length. Cirrus spinelets moderately sized, numerous rows, i.e. >20.

ETYMOLOGY

From *tetricus* L. = forbidding, refers to the *vagina dentata*.

REMARKS

The presence of pigment indicates this species resembles *T. simulator* (Haswell, 1924) and *T. novaezealandiae* (Haswell, 1888). *T. novaezealandiae* is said to contain 'a system of formidable chitinous teeth' (Haswell, 1924) and thus, on that account, differs substantially from the present species which has only fine teeth. *T. simulator* also has papillae which 'assume the appearance of teeth', but in the present species there can be little doubt that teeth, not papillae, are present.

The cirrus of the present species is long, slender and curved, so resembles that of *T. novaezealandiae* according to Haswell (1893: pl. XIII, figs 17-18), but not according to Fyfe (1942) who, dealing with *T. novaezealandiae* with prominent vaginal teeth, illustrates and states that the cirrus (penis) is L-shaped. Details of *T. simulator* are sketchy; however, Haswell (1924) stated 'the entire reproductive system closely resembles that of *T. comes*': certainly the cirrus of *T. comes* is much less slender with a more pronounced introvert than occurs in the present species.

The presence of nematodes in the testes of the present species echoes a similar observation made by Haswell (1893) with regard to *T. comes* who said 'many of them had parasitic Nematodes or their eggs or embryos lodged in the testes'.

Achenella n. gen.

Type species. Achenella sathonota n.sp.

Generic diagnosis. Temnocephalidae with 5 anterior tentacles, a single pair of testes posterior to the gut, genital organs contained in a connective tissue capsule, vesicular resorbens posterior - not pushing up into or adjacent to the gut, a rosette organ (a cluster of single cells subtending a small disc embedded in the epidermis) anterior to the excretory ampulla, and vitellaria clustered along the lateral margins of the gut.

Species included in Achenella. A. sathonota n.sp., *A. cougal* n.sp.

Etymology. From *achen* L. = poor, impoverished; pertaining to having only one pair of testes. Temnocephalidae has several genera with two or more pairs of testes.

Achenella sathonota n.sp.
(Figs 9,12a-d,f-i)

MATERIAL EXAMINED

HOLOTYPE: ex *Caridina indistincta* (Atyidae), Gully nr Capalaba, Brisbane (27.32°S, 153.12°E), 22 Sep. 1988, L. Cannon, Bouin's/Hx GL14589 (W).

PARATYPE: ex *Caridina indistincta* (Atyidae), Waterhole on creek at Henderson Rd, Sheldon, Brisbane (27.36°S, 153.13°E), 18 Mar. 1990, L. Cannon, Bouin's/H&E GL14591 (LS[1]).

OTHER MATERIAL: Queensland - same data as holotype, H&E GL14597 (LS[1]); same data as paratype, AFA/Haemalum GL14594 (W); Bouin's/Mallory's GL14596 (LS[1]); ex *C. indistincta* (Atyidae), Trib. of Scrubby Ck, Sheldon, Brisbane (27.37°S, 153.05°E), 2 Oct. 1991, I. Olsson, Hot water Form./Hx GL14598 (W); GL14599-14600 (LS[2,2]), ex *C. indistincta* (Atyidae), stream nr Kin Kin (26.16°S, 152.53°E), 23 Mar. 1990, L. Cannon & K. Sewell, AFA/Haemalum GL14583 (W), GL14584-5 (W); AFA/H&E GL14586 (LS[1]), AFA/H&E GL14587-8 (LS[1,1]). ex 'shrimp' (?*C. indistincta*) (Atyidae), Daisy Hill, Brisbane (27.28°S, 153.01°E), 16 Apr. 1989, L. Cannon, Bouin's/Hx GL14590 (W); SUSA/Hx GL14592; AFA/Hx GL14593 (W); ex 'shrimp' (?*C. indistincta*) (Atyidae), Bulimba Ck (27.33°S, 153.07°E), 18 Jul. 1979, A. Arthington, Form./unstained GL14595; NSW - ex *Caridina mccullochi*, tributary of Orara R., NSW (30.16.4°S, 153.03.1°E), 15 Feb. 1992, K. & S. Sewell,

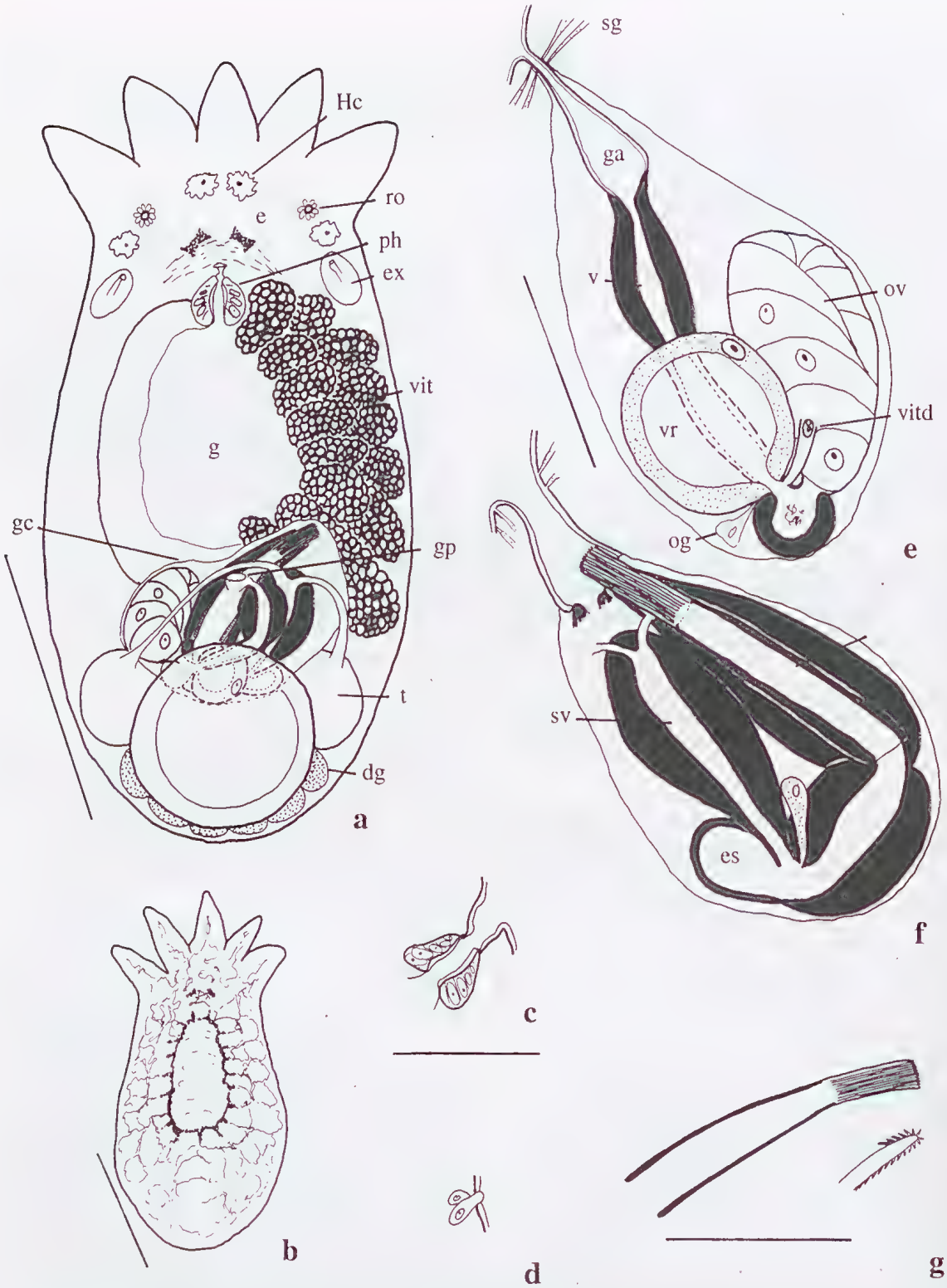


FIG. 9. *Achenella sathonota* n. gen., n.sp. a, internal anatomy of whole animal; b, dorsal pigment pattern; c, pharynx; d, rosette organ; e, detail female reproductive system; f, detail of male reproductive system; g, cirrus, and detail of spinelets. Scales: a,b, 250μm; c-d,e-f,g, 100μm.

Hot water Form./Haemalum GL14601 (W), GL14602 (W); Bouin's/H&E GL14603 (LS[1]),GL14606 (W); Bouin's/Hx GL14605, 14607 (W); Bouin's/H&E GL14608 (LS[1]).

DESCRIPTION

External characteristics. Body about 500-900μm (mean=710μm) long, and 250- 380μm (mean=330μm) wide [specimens from NSW slightly larger, to 1200μm long]; oval or elliptical, not dorso-ventrally compressed. Pigment extends to ventral surface (through parenchyma: especially dense about gut where it outlines the inner limits of the vitellaria). Posterior adhesive disc pedunculate: disc diameter 160μm at rim, disc peduncle 120μm across. Rosette organ about 50μm anterior to excretory ampulla. Epidermis syncitial, 5μm high dorsally, 9μm high ventrally. Cilia entirely absent.

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx conspicuous. Pharynx directed antero-ventrally, as wide as long, about 50μm across; very weak, undivided, with prominent cells within muscle blocks (though muscles barely discernible); lacking a non-cellular lip, with a conspicuous non-cellular lining, muscles not forming an obvious crenulate buccal rim. Pharynx sphincters equal but very weak. Oesophagus inconspicuous. Gut lacking colour, wider than long; without septa. Gastrodermis 50μm high. Gut contains eggs (of temnocephalan?), diatoms, cladocerans and nematodes.

Excretory system. Excretory pores lateral to mouth. Excretory ampulla a simple vacuole, thick walled, about 50×30μm in diameter. Major excretory ducts inconspicuous.

Nervous and sensory systems. Brain compact, transverse band. Major nerve trunks conspicuous ventrally. Eyes present, discrete, well separated (but joined by body pigment), about 20μm across. Eye pigment granules medium, even sized (about 1.5μm across), black-brown.

Glands. Rhabdite glands apparently a scatter of ventro-lateral glands about 20μm in diameter, with inconspicuous rhabdite tracts. Rhabdites only accumulate on tentacles (?). Haswell's cells conspicuous, four (a pair before brain, another before excretory pores) about 20μm across. Oesophageal glands inconspicuous (absent?). Ootype glands present. Shell glands in prominent lateral fields discharging to gonopore. Posterio-lateral glands inconspicuous (absent?). Disc glands prominent, a discrete eosinophilic cluster.

Muscles. Longitudinal muscles of body wall of equal size or strength dorsally and ventrally (and quite strong, about 3- 4μm wide). Circular muscles of body wall similar dorsally and ventrally (also 3-4μm wide). Dorso-ventral muscles and attachment muscles of pharynx weak. Attachment muscles of adhesive disc strong. Muscles controlling male organ strong (about stylet and seminal vesicle and also strong as dorso-lateral bands extending antero-lateral and postero-lateral from the region of the gonopore).

Reproductive system ♀. Gonopore mid-ventral, in posterior third of body. Genital atrium commodious. Ovary to about 50×90μm. Vesicula resorbens present, about 50×60μm, 210μm thick wall. Seminal receptacle single, hardly cut off from female canal. Vaginal teeth absent. Vagina long, compartmentalised (proximal region to about 75μm long with muscle walls 4μm thick, distal region to about 150μm long with walls 25μm thick). Vitellaria clumped, lateral (from excretory ampulla to testes - numerous large glands 75μm across).

Reproductive system ♂. Testes rounded, about 80μm in diameter, smooth. Vasa deferentia swollen, entering seminal vesicle separately. Seminal vesicle about 90×60μm, walls 20μm thick. Ejaculatory sac present. Prostate bulb separate, i.e. wider than cirrus base. Cirrus shaft gently curved. Cirrus hardly tapering, 170μm long, 25μm wide at base. Cirrus introvert swollen, but only very little, about 45μm or 1/4 of the cirrus length. Cirrus spines absent. Cirrus spinelets minute on a series of long sclerotic ridges, many rows i.e. >20.

ETYMOLOGY

From *sathon* Gr. = one with a large penis, referring to the relative size of the cirrus to body size.

REMARKS

Only one 5 tentacled species of temnocephalan has been described with one pair of testes, *Temnocephala brenesi* Jennings, 1968, from the shrimps, *Macrobrachium americanum*, in Costa Rica. The correct position of this species must await further study, but it does not appear to conform to *Achenella* n. gen.

In the present species the cirrus is slightly larger for specimens from Kin Kin and considerably larger (280μm long and 55μm wide at base) for those from *C. mccullochi* from NSW. This latter difference in size of the cirrus may reflect just bigger specimens or perhaps indicates these specimens from a different host and a distant

locality belong to a distinct species. Unless other differences become apparent all these specimens should be considered of the same species.

Achenella cougal n.sp.
(Fig. 10)

MATERIAL EXAMINED

HOLOTYPE: ex *Paratya australiensis* (Atyidae), Upper Currumbin Ck, Gold Coast (28.14.6°S, 153.20.8°E), 12 Apr. 1991, L. Cannon & K. Sewell, Hot water Form./H&E GL14581 (LS[2]).

OTHER MATERIAL: same data as holotype, Hx GL14582 (damaged W).

DESCRIPTION

External characteristics. Body about 950μm long, and 400μm wide; oval or elliptical, not dorso-ventrally compressed. Pigment confined to eyes. Posterior adhesive disc broadly pedunculate: disc diameter 180μm at rim. Rosette organ about 100μm anterior to excretory pores. Epidermis syncitial about 5μm high dorsally and ventrally. Cilia entirely absent.

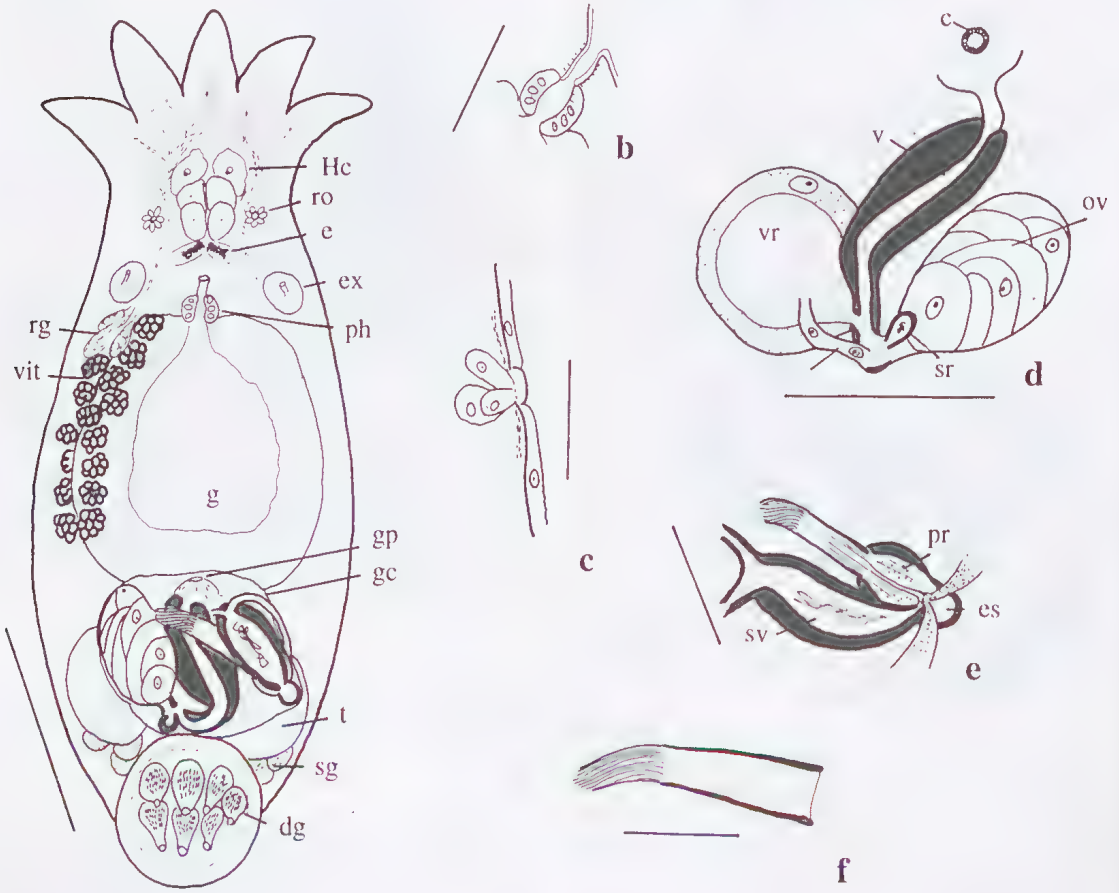
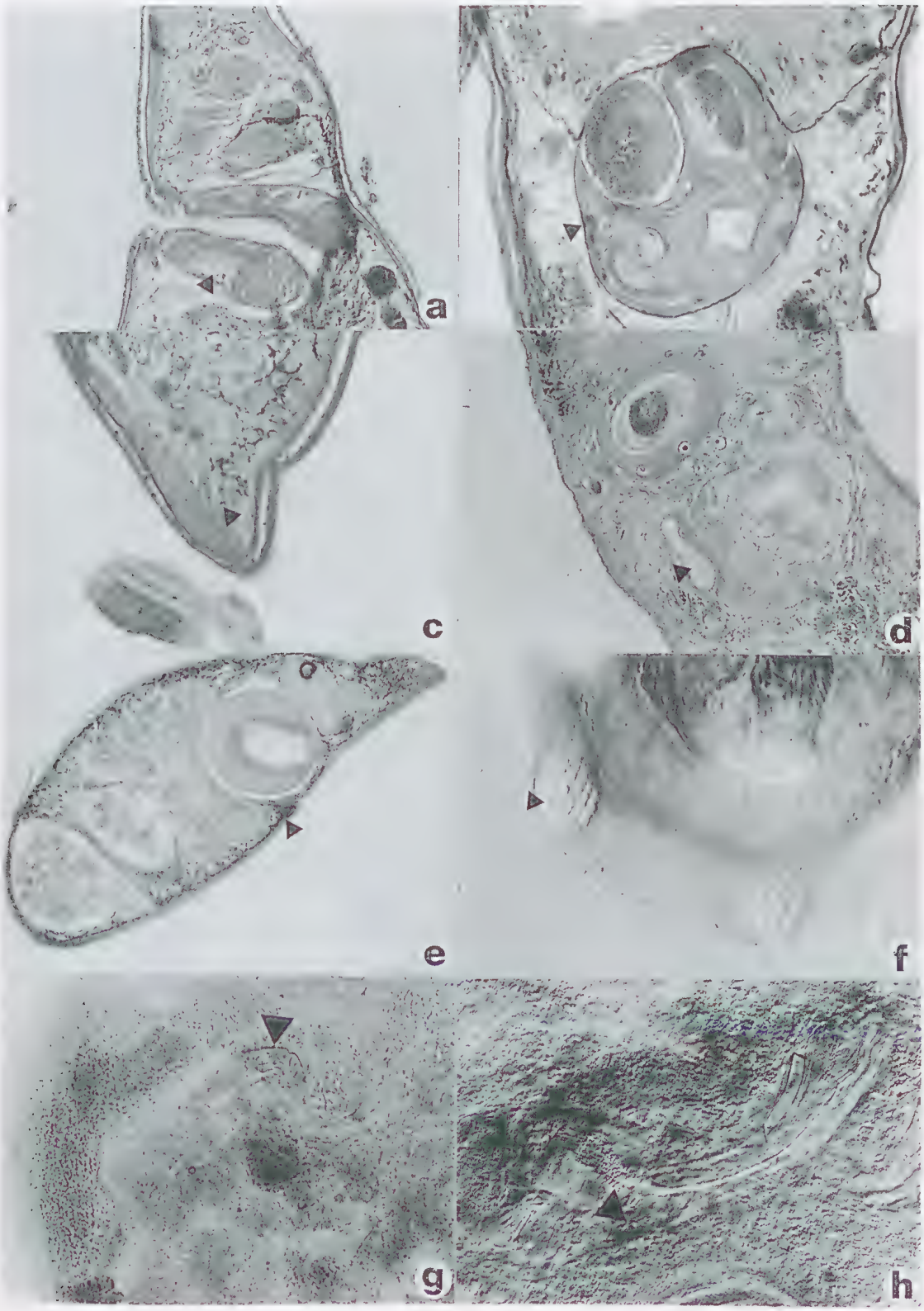


FIG. 10. *Achenella cougal* n.sp. a, internal anatomy of whole animal; b, pharynx; c, rosette organ; d, detail female reproductive system; e, detail of male reproductive system; f, cirrus. Scales: a, 250μm; b, 100μm; c, 50μm; d-e, 100μm; f, 50μm.

FIG. 11. Photomicrographs of new temnocephalans from crabs and shrimps. a-c, *Temnocephala athertonensis* n.sp.: a, pharynx showing prominent cells between sphincter blocks; b, genital capsule; c, weak postero-lateral glands; d, *Temnocephala butlerae* n.sp. genital region showing prominent ejaculatory sac; e, *Temnocephala improcera* n.sp. showing simple muscular pharynx: note pigment below body wall; f, *Temnocephala neqae* n.sp. posterior end showing prominent postero-lateral glands; g, *Temnohaswellia pugna* n.sp. cirrus; h, *Temnohaswellia tetrica* n.sp. showing shaft of cirrus and vaginal teeth, overlaying the introvert. Scales: 1cm = 100μm (a,b,e,g,h); 1cm = 50μm (c,d,f). Nomarski f,g,h.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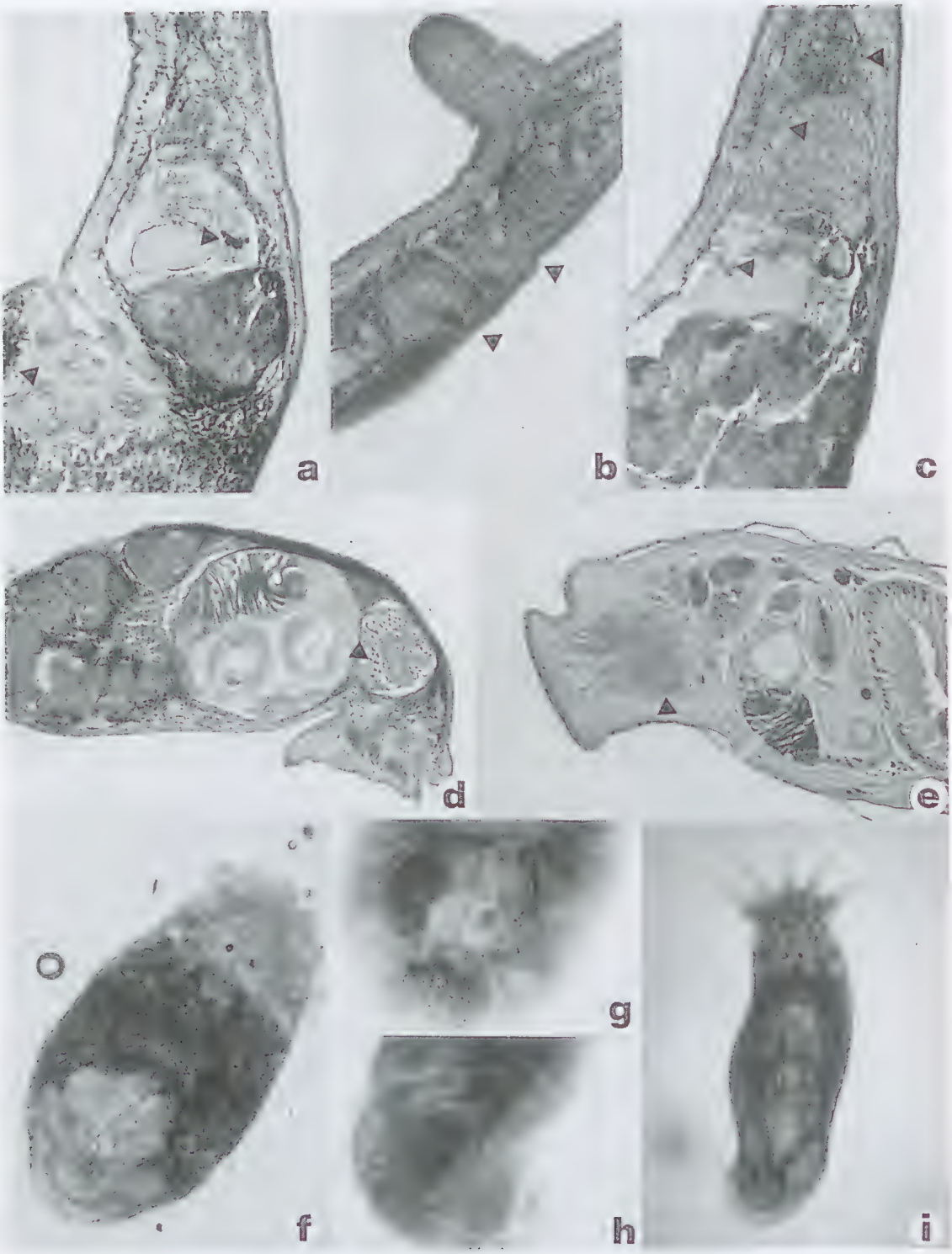
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Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx conspicuous (muscular, about 50μm deep). Pharynx directed antero-ventrally, as wide as long, about 72μm in diameter; weak, undivided, with prominent cells within muscle blocks; lacking a non-cellular lip, with a conspicuous non-cellular lining, muscles not forming an obvious crenulate buccal rim. Pharynx sphincters equal (very little musculature). Oesophagus inconspicuous. Gut lacking colour, as wide as long; without septa. Gastrodermis about 70μm high.

Excretory system. Excretory pores lateral to mouth. Excretory ampulla a simple vacuole, thick walled (12- 15μm), about 50μm in diameter. Major excretory ducts inconspicuous.

Nervous and sensory systems. Brain bilobed (with large bilobed ?forebrain). Eyes present, discrete, well separated, about 30-40μm across. Eye pigment granules medium, even sized, about 2μm, black-brown to red-black.

Glands. Rhabdite glands in lateral fields anterior to anterior testes (and anterior and lateral to pharynx), few, less than 10 each side; 15-25μm in diameter, with rhabdite tracts to base of tentacles. Rhabdites only accumulate on tentacles. Haswell's cells conspicuous, two together before ?forebrain, about 70×30μm. Oesophageal glands and ootype glands inconspicuous (absent?). Shell glands present postero-lateral to testes open to gonopore. Postero-lateral glands absent. Disc glands prominent, scattered around testes with a cluster of deeply eosinophilic club shaped cisternae opening on to disc.

Muscles. Longitudinal muscles of body wall stronger ventrally. Dorso-ventral muscles and attachment muscles of pharynx weak. Attachment muscles of adhesive disc and muscles controlling male organ strong.

Reproductive system ♀. Gonopore mid-ventral, in posterior third of body. Genital atrium large. Ovary about 130×80μm. Vesicula resorbens present, about 90μm across, 15μm thick wall. Seminal receptacle single, about 20μm across. Vaginal teeth absent. Vagina long, compartmentalised, distally muscular 145μm long walls 25μm thick, proximally 40μm long walls 7-8μm thick. Vitellaria discrete (scattered), lateral about 20μm across.

Reproductive system ♂. Testes a single pair, rounded, about 140μm in diameter, smooth, posterior to gut. Vasa deferentia swollen (to about 20μm), entering seminal vesicle separately. Seminal vesicle about 100×70μm with thick (10μm) walls. Ejaculatory sac present about 50μm in diameter, with wide neck (joins directly to back of prostate bulb). In holotype a very large prostate gland (110-125μm across) lies anterior to testes. Prostate bulb incorporated, i.e. continuation of cirrus base. Cirrus shaft straight. Cirrus hardly tapering, 100μm long, 20μm wide at base. Cirrus introvert not swollen, about 40μm long tapering to 10μm wide; 1/3 of the cirrus length. Cirrus spines present, on about 20 strong ribs spiralling out.

ETYMOLOGY

The specific name refers to the name of the locality. Currumbin Ck rises in Cougal National Park.

REMARKS

The lack of pigment in the body and the much smaller, more gracile cirrus serve to clearly distinguish this species from the only other member of the genus *A. sathonota.*

Achenella sp.

MATERIAL EXAMINED

ex *Austratya striolata* (Austratyidae); Yuccabine Ck, Kirrama (18.13°S, 145.45°E), 10 Jul. 1985, R. Smith, Bouin's/H&E GL14557 (TS[3]).

DESCRIPTION

External characteristics. Body about 500μm long, and 400μm wide; oval or elliptical, not dorso-ventrally compressed. Pigment confined to eyes. Posterior adhesive disc pedunculate: disc diameter 140μm at rim, disc peduncle about 90μm across. Epidermis about 7μm high dorsally and ventrally. Cilia entirely absent (?).

Alimentary system. Mouth mid-ventral in anterior quarter of body. Buccal cavity or prepharynx inconspicuous. Pharynx directed antero-ventrally (?), as wide as long, about 70μm in diameter; weak, with nucleate cells within muscle blocks (?); without a conspicuous non-cellular lining.

FIG. 12. Photomicrographs of new temnocephalans from crabs and shrimps. a-d,f-i, *Achenella sathonota* n. gen., n.sp. a, weak pharynx, brain and eye; b, excretory pore and anterior to it the rosette organ; c, brain, ?forebrain and Haswell's cell; d, genital capsule and posterior testis; e, *Achenella cougal* n.sp. genital capsule and prominent cisternae of disc glands with a weakly pedunculate adhesive disc; f, specimen from Capalaba; g, posterior showing cirrus, specimen from Stretton; h, posterior (lateral) showing cirrus, specimen from Kin Kin; i, specimen from Orara R., NSW. Scales: 1cm = 50μm (a-c); 1cm = 100μm (d,e,g,f); 1cm = 250μm (f,i).

Pharynx sphincters equal (?). Gut lacking colour, as wide as long (?). Gastrodermis about 40μm high.

Excretory system. Excretory pores lateral to mouth. Excretory ampulla a simple vacuole, thick walled (20μm), about 35-40μm across. Major excretory ducts inconspicuous.

Nervous and sensory systems. Brain compact, transverse band. Major nerve trunks inconspicuous. Eyes present, discrete, well separated, about 25×20μm. Eye pigment granules medium, even sized, red-black.

Glands. Rhabdite glands in lateral fields anterior to anterior testes (?); about 15μm across. Shell glands present. Disc glands prominent, a discrete cluster.

Muscles. Longitudinal muscles of body wall of equal size or strength dorsally and ventrally. Circular muscles of body wall similar dorsally and ventrally. Dorso-ventral muscles weak; attachment muscles of pharynx and of adhesive disc weak. Muscles controlling male organ strong, about 25μm thick.

Reproductive system ♀. Gonopore mid-ventral, in posterior quarter of body. Genital atrium commodious. Ovary about 50×70μm. Vesicula resorbens present, about 75μm in diameter, about 20μm thick wall. Vagina chambered and strongly muscular. Egg capsules ovoid or pyriform, about 225μm in diameter; attached on side without stalk, on cephalothorax (inside branchial chamber).

Reproductive system ♂. Testes rounded. Seminal vesicle about 50μm across. Ejaculatory sac present, with narrowed neck? Cirrus shaft straight. Cirrus hardly tapering, 100μm long, 32μm wide at base. Cirrus introvert not swollen, about 10μm long or 1/9 of cirrus. Cirrus spinelets minute, few rows, i.e. <20.

Remarks

This one sectioned specimen is tentatively placed in *Achenella* as there appears but one pair of testes, the genital organs are in a capsule and disc glands are prominent. Until better material is available it is not appropriate to provide a specific name.

ACKNOWLEDGEMENTS

I wish to acknowledge the generous support of the Australian Biological Resources Survey and the considerable help in the field from Mr Kim Sewell. For help in the laboratory I am indebted to Lucille Gillespie and especially Christine Lee. John Short provided confirmation of identification of the various hosts. Thanks are also extended to Leigh Winsor, James Cook University, and Stephen Cook, Queensland Museum for some specimens.

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NOTES ON *PARMULARIA* MACGILLIVRAY (BRYOZOA: CHEILOSTOMIDA) FROM AUSTRALIA

P.J. CHIMONIDES AND P.L. COOK

Chimonides, P.J. & Cook, P.L. 1993 06 30: Notes on *Parmularia* MacGillivray (Bryozoa: Cheilostomida) from Australia. *Memoirs of the Queensland Museum* 33(1): 41-48. Brisbane. ISSN 0079-8835.

Colonies of *Parmularia* form leaf-like lobes, anchored above the surface of particulate sea-bottoms by a wide, turgid, extrazooidal rhizoid system. In spite of this distinctive colony form, species generally show striking similarities with those of two normally encrusting genera, *Emballotheca* Levinsen and *Calyptotheca* Harmer, and all three genera are here included in the family Parmulariidae Canu & Bassler. Four species, *P. obliqua* (MacGillivray), *P. quadlingi* (Haswell), *P. arnoldi* sp.nov. and *P. occidenta* sp.nov. are described. □ *Bryozoa, Parmularia, Cheilostomida, Parmulariidae, Emballotheca, Calyptotheca, new species.*

Pantelakis J. Chimonides, Zoology Department, The Natural History Museum, Cromwell Rd, London SW7 5BD, United Kingdom; Patricia L. Cook, Associate, Museum of Victoria, Swanston St, Melbourne, Victoria 3000, Australia; 16 March, 1993.

Parmularia was introduced by MacGillivray (1887) who quoted a manuscript name mentioned in correspondence by George Busk. The distinctive leaf-like colonies, with large rhizoid systems, which support them above the surface of the substratum, are well-known in Recent Australasian bryozoan sand-faunas; fragments of colonies frequently occur in fossil assemblages from the Tertiary of Victoria. Living specimens have been described by Maplestone (1910), Bock (1982) and Cook & Chimonides (1985), all of whom particularly noted the brilliant red and orange pigments of embryos and coelomic tissues. Recognition of the genus is relatively easy, even from fragmented specimens, as the astogenetic pattern is a simple but distinctive one, and the ontogenetic changes during colony life are not profound.

Lanceopora d'Orbigny (1852) was introduced for Recent *L. elegans* from Malacca (d'Orbigny, 1852: 187(bis), pl.680, figs 7-10), and is almost certainly a senior synonym of *Parmularia*. D'Orbigny's figures of *L. elegans* depict the budding pattern (including the marginal kenozooidal and extrazooidal structures) and show circular orifices of autozooids surrounded by a distinct raised peristome. The range of orifice shapes is wide among species assigned to *Parmularia* and *Lanceopora*. This range is so wide, the orifice shape might be a useful, subgeneric character. The circular orifices were fully discussed by Harmer (1957), who was undecided as to the synonomy of the two generic names (see Hastings in Harmer, 1957: 983 footnote).The type specimen of *L. elegans* no longer exists (Canu & Bassler, 1929: 398). The type colony was minute (less than 4mm long) and sexually immature, without any ovicells.The species will probably never be recognized again with certainty, especially as several different species of *Lanceopora* are known from the Indonesian and Australasian regions. Unlike *L. elegans*, the first Australian *Parmularia* had distinctly sinuate orifices. Until a neotype for *Lanceopora* is chosen, and in view of the frequent use of *Parmularia* in Australian literature, the species discussed here are referred to *Parmularia*.

Specimens were bleached in sodium hypochlorite solution and coated with AuPd for SEM. Abbreviations used: BMNH, Natural History Museum, London; WAM, Western Australian Museum; QM Queensland Museum.

STRUCTURE OF *PARMULARIA* COLONIES

Colonies appear to be bilaminar, the zooid ofifices opening on identical faces. There is only a single, central lamina, which is a basal wall common to both zooidal expanses. The lamina is pierced by septulae which allow communication between zooids of either face (Cook & Chimonides, 1985: fig. 4). Usually, at the earlier astogenetic stages, the colony is lanceolate, with several distally budded series. In several species, this is followed by lateral and disto-lateral series, which eventually form a discoid or trilobed colony. Zooids at the margins, especially where further growth has ceased, are usually kenozooids,

formed by basal calcified lamina, and shallow lateral walls, with a cuticular frontal wall. Towards the colony's base (the earlier astogenetic regions), these kenozooids become extrazooidal, as the lateral walls are marginally deficient. They form a narrow band of turgid coelomic tissue, bounded by cuticle and communicating with the extrazooidal rhizoid system. Later in astogeny, this system may produce extensions that form secondary rhizoids (Harmer, 1957).

In life, quite large colonies (4cm in diameter) are supported several centimetres above the bottom sediment by the wide, turgid, extrazooidal rhizoid, which is deeply buried, and divided terminally into numerous rootlets with adhesive cuticle. Calcification of the extrazooidal structures surrounding the origin of the rhizoid becomes much changed during ontogeny. The area becomes thickened by calcification, and is partitioned into a complex of partially opened chambers (Canu & Bassler, 1929; Harmer, 1957). At no time is communication between the zooids and the rhizoids interrupted because damaged rhizoids can be repaired and their turgidity regained (Cook & Chimonides, 1985, fig. 2).

The frontal shield of all autozooids consists of an interior, cryptocystidean calcified wall, overlain by a hypostegal coelom and bounded by frontal cuticle. Frontal septulae, which communicate with the visceral coelom, are placed marginally, especially at the distal and proximal corners of zooid frontals (Cook & Chimonides, 1981, 1985). Other pores are present in the frontal calcification, which may be thickened during ontogeny, particularly round the orifice, which then becomes sunken and obscured. The frontal calcification may be tuberculate, rising into suboral mucros in some species.

Autozooids are monomorphic, becoming larger with astogeny; their orifices may be variously rounded or sinuate proximally, with or without condyles and spinous outgrowths. Brooding zooids are produced fairly late in astogeny, and often have larger, wider orifices than the autozooids, although the kind and degree of dimorphism varies from species to species. Ovicells are prominent; the outer calcification formed from proximally directed outgrowths from the frontal shields of two or more autozooids placed distally to the maternal zooid which produces the egg. Ovicells often show distinct 'suture lines' (Harmer, 1957), which may indicate the number of distal contributory zooids. Ovicells are closed by the brooding zooid operculum, although the position of the operculum varies with preservation and the developmental state of the ovicells. Several species possess large, interzooidal avicularia, which may have triangular or rounded mandibles, but adventitious avicularia have not been reported.

SYSTEMATICS

Family relationships of *Parmularia* have been discussed by Harmer (1957: 985, 1087, footnote), who discounted an earlier suggestion by Livingstone (1928) that the genus had a close relationship with *Emballotheca* Levinsen. Harmer reasoned that the orifices in *Parmularia* were sinuate (unlike those of *Emballotheca*) and the colony growth forms were totally dissimilar in the two genera. The orifice shape of all species of *Emballotheca* is admittedly non-sinuate, but, as shown below, not all species of *Parmularia* have sinuate orifices. The kinds and degree of dimorphism of brooding zooids, and the structure of the ovicells is the same in both *Emballotheca* and *Parmularia* and, in these characters, both genera greatly resemble a third genus, *Calyptotheca* Harmer. However, there is a continuity among variable characteristics in all three genera, and Dumont (1981) has discussed the difficulties that have arisen from past attempts to define, or distinguish between, *Emballotheca* and *Calyptotheca*. *Calyptotheca* was introduced by Harmer (1957: 1008) to accommodate species with a sinuate or rounded orifice, which had previously been assigned to *Emballotheca*. Surprisingly, he did not discuss the similarities between *Calyptotheca* and *Parmularia*, particularly as *Calyptotheca* possessed sinuate orifices, the supposed distinction between *Parmularia* and *Emballotheca* (see above).

A further similarity between some species of *Calyptotheca* and *Parmularia* is the occurrence of large, interzooidal avicularia. These heterozooids have mandibles with robust sclerites and, in some cases, possess lophophores and viscera. Their function is unknown. Interzooidal avicularia occur in *Calyptotheca capitifera* (Canu & Bassler, 1929), *C. conica* Cook (1965), *Calyptotheca* sp. Harmer (1957), *Parmularia quadlingi* (Haswell, 1880, according to Livingstone, 1926) *P. cylindrica* (Canu & Bassler, 1929, according to Harmer, 1957) and *P. occidenta* sp.nov. Adventitious avicularia occur in most species of *Emballotheca* and *Calyptotheca* but, as noted, are apparently completely absent in *Parmularia*.

Although the colony form of *Parmularia* differs from that of all species of *Emballotheca*,

which is encrusting, it is of interest that several species of *Calyptotheca* exhibit equally distinctive, but different, adaptations of growth which are associated with life in a sand-fauna environment. Lunulitiform, rooted colonies occur in *C. orbicularis* Harmer and *C. circularis* Harmer (Harmer, 1957) and lunulitiform, unrooted colonies in *C. conica* Cook (1965).

A similar diversity of colony form, which also includes different kinds of adaptation to a sand-fauna existence, occurs in the Microporellidae (*Microporella, Flustramorpha* and *Diporula*: Cook, 1968; Hayward & Cook, 1983), Celleporariidae (*Celleporaria* and *Sphaeropora*: Harmer, 1957; Cook & Chimonides, 1981), Eurystomellidae (*Eurystomella* and *Selenariopsis*: Cook & Chimonides, 1981), and Petraliellidae (*Mucropetraliella* and *Riscodopa*: Cook & Chimonides, 1981; Gordon, 1989). In all respects other than colony form, the three genera *Emballotheca, Calyptotheca* and *Parmularia* comprise a fairly natural grouping that differs from other groups of genera often included informally in the family Schizoporellidae in the structure of the ovicells and the frequency of dimorphism of the brooding zooids.

Class GYMNOLAEMATA Allman, 1856
Order CHEILOSTOMIDA Busk, 1852
Family PARMULARIIDAE Canu & Bassler, 1927

Parmulariidae Canu & Bassler, 1927: 21,35.
Lanceoporidae Harmer, 1957: 983.

Type genus. Parmularia MacGillivray.
Genera included. Parmularia MacGillivray, 1887, *Lanceopora* d'Orbigny, 1852, *Emballotheca* Levinsen, 1909 and *Calyptotheca* Harmer, 1957.

Description

Cryptocystidean Ascophora with primary orifice rounded distally, but variable proximally; spines absent. Brooding zooid orifices usually dimorphic, large and wide. Ovicells usually formed by proximal extensions of calcified frontal shields of more than one distal zooid. Adventitious and interzooidal avicularia present or absent.

Remarks

Canu & Bassler (1927) introduced Parmulariidae, in spite of their use of 'Parmulariidae Maplestone 1912' as a reference, both in 1927 and in 1929 (p.397). This misquotation of the authorship was followed by Wass & Yoo (1983: 340) but it should be noted that Harmer (1957: 983) ascribed the family name to Canu & Bassler. Maplestone used *Parmularia* in 1910 and 1913: a work dated 1912 does not seem to exist.

Parmularia MacGillivray, 1887

Parmularia MacGillivray 1887: 191,211.
Lanceopora d'Orbigny: Harmer, 1957.

Type species. Eschara obliqua MacGillivray, 1869.

Description

Colonies erect, compressed, leaf-like, with orifices opening on both faces, supported by one or more turgid, extrazooidal cuticular rhizoids. Autozooids with orifices straight, rounded or sinuate proximally. Brooding zooids with larger, often distinctly dimorphic orifices. Adventitious avicularia absent; interzooidal avicularia sometimes present.

Remarks

Harmer (1957) gave a key to Indo-west Pacific species and introduced *Lanceopora formosa* (Harmer, 1957:987, pl.66, figs 10-13, 103-105), an elongated, lanceolate, very delicate species from the East Indes. He also redescribed *L. cylindrica* Canu & Bassler (1929) from the Philippines and somewhat doubtfully assigned his own Siboga material, which had interzooidal avicularia, to this species.

Schizoporella flabellata Maplestone (1902: 68, pl. 7, fig. 10), from the Tertiary of Victoria, was later included in *Parmularia* by Maplestone (1910, 1913). Ovicells do not seem to have been described in fossil specimens, which are usually fragmented or very small and sexually immature. The degree of dimorphism of the Tertiary species is therefore unknown, but the small, distinct, rounded sinus of the autozooid orifice has usually been taken as an indication of a close relationship between *P. flabellata* and *P. obliqua*, the Recent type species of *Parmularia* (see Livingstone, 1924:190). Stach (1935) referred his Lower Pliocene Australian specimens to *P. obliqua.*

Parmularia obliqua (MacGillivray)
(Fig. 1a)

Eschara obliqua MacGillivray, 1869: 137. 1880: 39, pl. 48, figs 1, 1a, 1 b.
Parmularia obliqua MacGillivray, 1887: 211. Maplestone, 1910: 42, pl. 10. 1913: 360, pl. 28, fig.

11. Livingstone, 1924; 190, pl. 23, figs 1,2, pls 25,26, figs la-c. Stach, 1935: 343 , pl. 12, fig. 5. Wass & Yoo, 1983: 340, figs 60-61. Cook & Chimonides, 1985: 72, fig. 1.

Schizoporella flabellata Maplestone, 1902: 68, pl. 7, figs 10, 10a.

Lanceopora obliqua Harmer, 1957: 990, fig. 102. cum.syn. Bock 1982: 383, figs 9, 28a,b, pl.28.6.

MATERIAL EXAMINED

BMNH: 1884.11.4.14, Port Phillip; 1899.5.1.1080, Curtis Is., Bass Strait; 1899.7.1.43 & 84, Port Phillip, Victoria; 1912.5.1.3A, South Australia; 1965.2.2.1, Holothuria Bank, northwestern Australia, 44-62m (with *P. occidenta* q.v.); 1975.7.28.29, off Adelaide, 36-64m; 1987.1.10.2, off Jurien Bay, Western Australia, 137m. WAM: off Jurien Bay, Western Australia 137m.

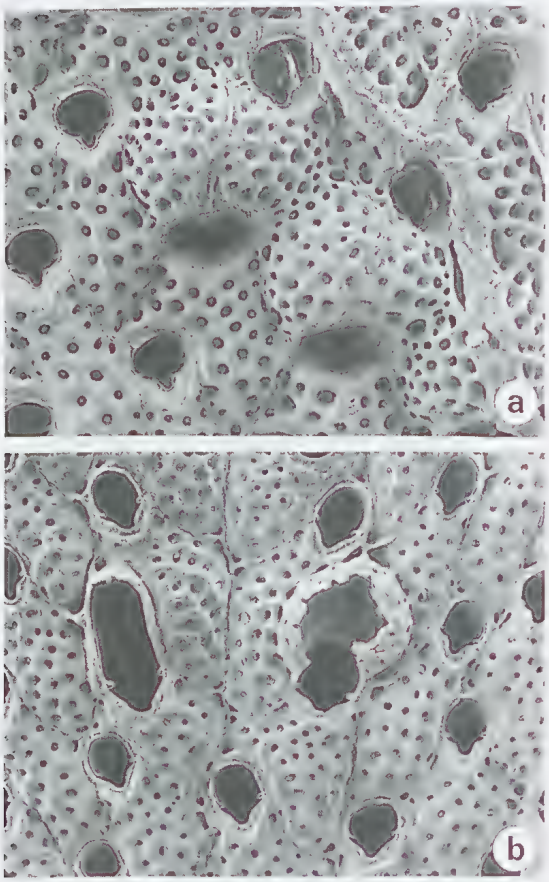

FIG. 1. a, *Parmularia obliqua*, Jurien Bay, autozooids and brooding zooids, ×57. b, *P. quadlingi*, Townsville, autozooids and one broken ovicell of brooding zooid, with one vicarious avicularium, ×49.

DESCRIPTION

Colonies kidney-shaped or nearly circular; wide, up to 4cm in diameter. Little evidence of an early lanceolate form. Autozooid orifices with very small, triangular-to-rounded proximal sinus and large, paired condyles. Brooding zooid orifices often large, wide and slit-like, sometimes with paired distal, but proximally directed, processes. Ovicells often very large, produced late in astogeny, with suture lines. Interzooidal avicularia absent.

REMARKS

P. obliqua has been reported from the coasts of Victoria, South Australia and Western Australia. With such a large distribution, some variation in characters may be expected. This seems to be most expressed in the degree of dimorphism of the brooding zooids. Specimens illustrated by Bock (1982) and Wass & Yoo (1983) show very wide, almost slit-like orifices of brooding zooids. The colonies from Jurien Bay have more open, proximally curved brooding zooid orifices, but a similar small autozooid sinus (Fig. 1a). Some specimens show a wide range of variation within a single colony.

Parmularia quadlingi (Haswell)
(Fig. 1b)

Lepralia (Schizoporella) quadlingi Haswell, 1880: 39, pl. 2, fig. 2.

Parmularia quadlingi Livingstone, 1926: 85, pl. 5, fig. 6, pl. 6. figs 1-2.

Lanceopora quadlingi Harmer, 1957: 990, pl. 66, fig. 11 c, 18, fig. 106.

MATERIAL EXAMINED

BMNH: 1910.6.16.5 (labelled 'Co-type'), Holborn Is., Queensland; 1935.2.22.1, Torres Strait; 1975.7.28.27, Torres Strait (figured by Harmer, 1957); 1975.7.28.28 (labelled 'from collection described by Haswell'), Port Denison, Queensland; 1987.1.10.1, off Townsville, Queensland, 1981, P. Arnold.

DESCRIPTION

Colonies lanceolate at first, becoming trilobed, up to 2cm in diameter. Autozooids with a small rounded or subtriangular sinus. Brooding zooid orifices larger. Interzooidal avicularia with an elongated, subtriangular mandible present.

REMARKS

Livingstone (1926) redescribed *P. quadlingi* from Haswell's 'type' (specimen in the Austra-

lian Museum, Sydney) and from his own material which was also from Queensland (and which possessed rhizoids). He noted that the 'type' specimen was fragmentary, and that it did not include any large, interzooidal avicularia. The autozooid orifices, each with a small, rounded,

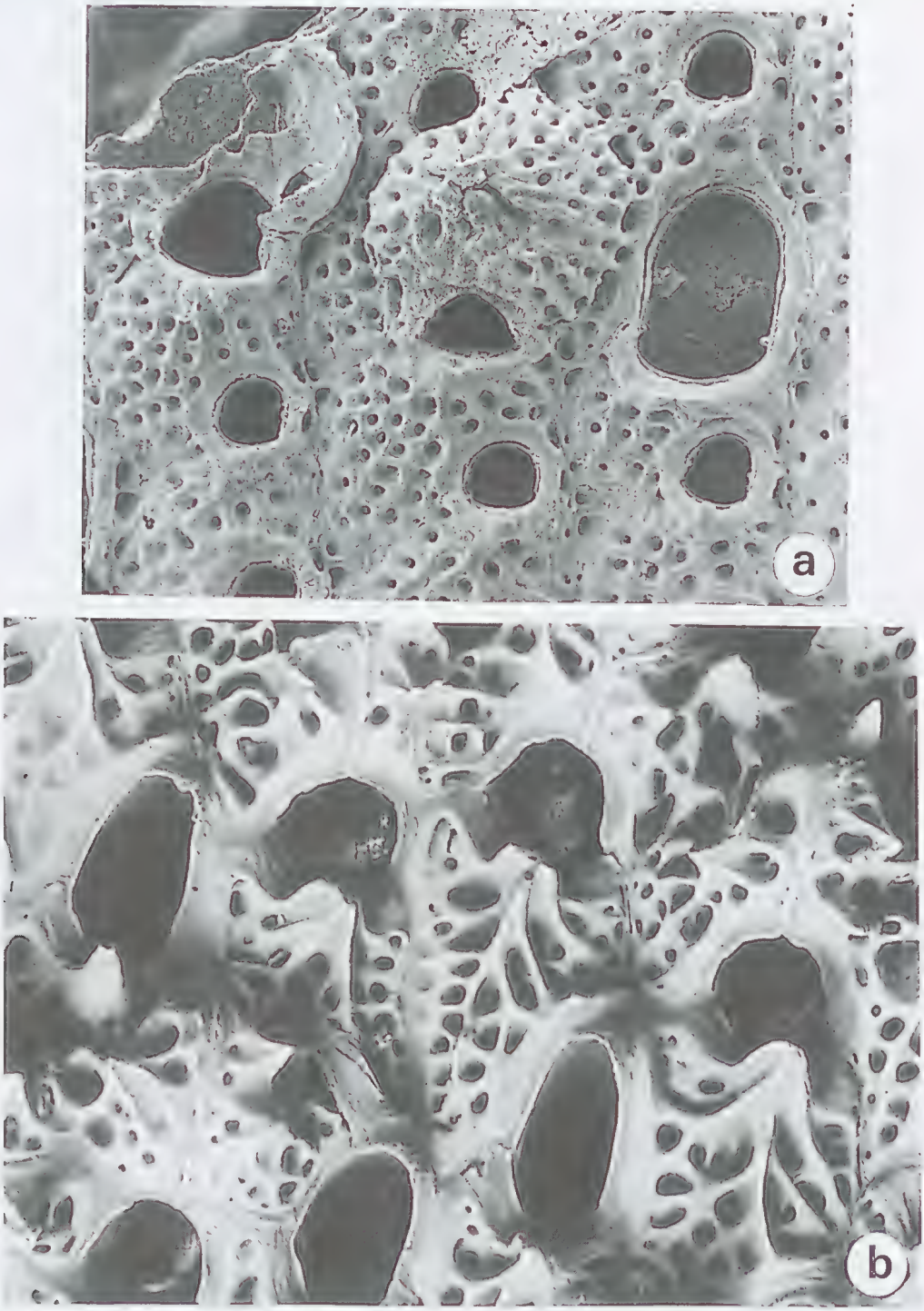

FIG. 2. a, *Parmularia occidenta*, Holothuria bank, autozooids, one brooding zooid and one vicarious avicularium, ×73. b, *Parmularia arnoldi*, Townsville, autozooids and brooding zooids with ovicells, ×85.

proximal sinus, illustrated by Livingstone (1926) are similar to those figured by Haswell (1880). Furthermore, both illustrations show similar ovicells and relatively little dimorphism of the brooding zooid orifices.

The BMNH 'Co-type' (1910.6.16.5) is a minute fragment comprising 8 zooids and 4 brooding zooids. It differs from Livingstone's figure in having larger autozooid orifices with subtriangular sinus and distinct condyles. No interzooidal avicularia are present. There is, however, some dimorphism of brooding zooid orifices. Harmer's figure (1957: pl. 66, fig. 18) shows autozooids with orifices resembling those figured by Haswell and Livingstone. However, the one brooding zooid orifice shown has a wide proximal curved edge with no sinus. Material from the same collection (Haddon) and locality (Torres Strait) in the BMNH (1935.2.22.1), which was also examined by Harmer, shows that the shape of the autozooid orifice may change with astogeny. The autozooids nearer the growing edge may have orifices with a wide subtriangular sinus. The brooding zooid orifices are larger and have a wider sinus which can be obscured by raised proximal calcification. The interzooidal avicularia resemble Livingstone's figure.

The specimen from Townsville (BMNH 1987.1.10.1, Fig. 1b) also has autozooid orifices with a subtriangular sinus, and a dimorphism of the brooding zooids is evident. The mandible of the interzooidal avicularia are proportionally much longer than those illustrated by Livingstone (1926: pl. 6, fig. 1) and by Harmer (1957: pl. 66, fig. 18). With this wide range of variability, *P. quadlingi* sensu lato may include the Siboga specimens from the Sulu Archipelago, which Harmer (1957) assigned to *P. cylindrica*. *P. cylindrica* Canu & Bassler (1929) was not described with interzooidal avicularia and none are present in the material examined (*P. cylindrica*, Bassler Collection BMNH 1931.12.30.153, Philippines). The interzooidal avicularia figured by Harmer seem to have had very short triangular mandibles and, like those of *P. quadlingi*, are narrower than those of *P. occidenta*.

P. quadlingi may prove to be a complex of more than one form or a single variable species. It appears to be confined to the coast of Queensland and the Torres and Makassar Straits.

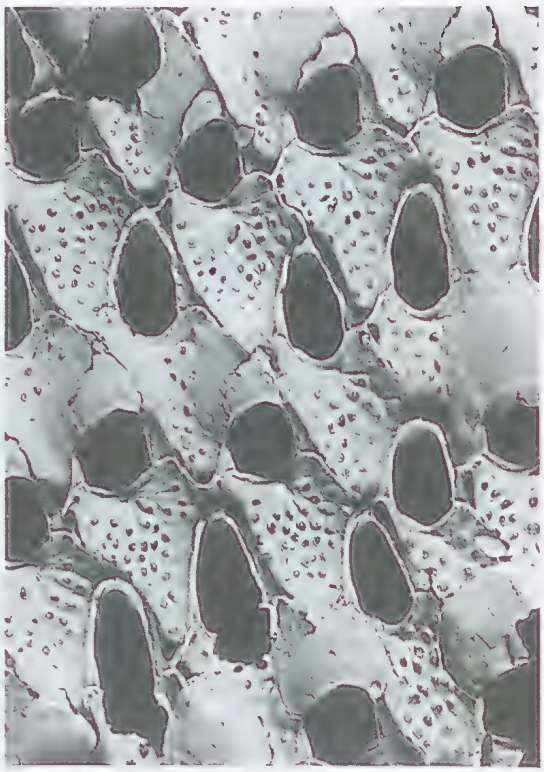

FIG. 3. *Parmularia arnoldi*, Townsville, autozooids and maternal brooding zooids with incipient ovicell development, ×48.

Parmularia occidenta sp.nov.
(Fig. 2a)

MATERIAL EXAMINED

HOLOTYPE: BMNH 1892.1.28.40A, Holothuria Bank, northwestern Australia, 27m.

PARATYPES: BMNH: 1892.1.28.40B, as for holotype; 1987.1.10.3, Holothuria Bank, 44-62m, (with *P. obliqua*.

ETYMOLOGY

Latin *occidentis*, west.

DESCRIPTION

Colonies lanceolate in early astogeny, becoming discoid or reniform, up to 2cm wide, with laterally directed zooidal series and zones of ovicells. Autozooid orifices somewhat elongated, curved, but not sinuate proximally, with small, spine-like, paired condyles near the proximal margin. Brooding zooid orifices wide, slightly curved proximally. During ontogenetic thickening a mucronate process develops proximally to the orifice and a similar mucro may appear on the

frontal surface of the ovicell. Interzooidal avicularia very large and wide, but with a short, narrow frontal shield that forms a raised shelf proximal to the mandible. Mandibles large, wide, rounded distally, with robust paired sclerites.

REMARKS

The holotype colony is dry but has a well developed extrazooidal calcification indicating that the rhizoid would have been 7mm wide at its origin. The accompanying paratype colony is only 1cm wide but has a rhizoid >1cm long and 2mm wide at its origin. The interzooidal avicularia often develop mandibles late in ontogeny and may be seen in a partially developed condition at some distance from the growing edge. *P. occidenta* resembles *P. mcneilli* Livingstone (1924: 194, pl. 24, figs 1,2, pl. 25, fig. 2), but differs by very large interzooidal avicularia. *P. occidenta* is known only from NW Australia.

Parmularia arnoldi sp.nov.
(Figs 2b, 3)

Parmularia sp. Cook & Chimonides, 1985:71, figs 2, 3A,B.

MATERIAL EXAMINED

HOLOTYPE: QM G21260, off Townsville, Queensland, 10-15m, large specimen 28mm in length with rootlet.

PARATYPES: QM: G21261, as for holotype colony fragements; G21259, Cleveland Bay, Queensland (19°13'S, 146°58'E), 23 August 1986, P.Arnold & A. Birtles, two colony fragment. BMNH: 1986.7.30.1, off Townsville, Queensland, 10-15m, numerous colony fragments, some with rootlets.

ETYMOLOGY

For Peter Arnold, Museum of Tropical Queensland.

DESCRIPTION

Early astogenetic stages lanceolate. Colonies becoming large, >4cm in diameter, discoid or reniform. Autozooid orifices very elongated, narrowing distally, deeply curved proximally, but without a distinct sinus; lateral condyles small. Distal rim of orifice raised, often with thin, crenulated processes overhanging the operculum. During ontogeny, a long mucronate process is developed proximally that obscures the secondary orifice. Brooding zooid orifices not elongated, slightly wider and proximally sinuate. Ovicells very large, with two or three suture lines, becoming tuberculate with large processes on the frontal surface. Avicularia absent.

REMARKS

The autozooid orifices distinguish this species from all others. The similarity between the autozooids of *P. arnoldi* and the avicularian zooids of *P. quadlingi* is striking (cf. Figs 1b, 2b). The raised distal process in *P. arnoldi* often overhangs the orifice and is reminiscent of the similar processes which occur in the dimorphic zooids of *Uscia mexicana* Banta (1969; see also Cook, 1979). The minute peg-like condyles are present in both autozooids and brooding zooids of *P. arnoldi*. Apart from not being as elongated, the brooding zooid orifices are not very dimorphic, being only slightly wider and having a shallow proximal sinus. Autozooids and brooding zooids frequently occur in sloping or horizontal series of alternating astogenetic generations (Fig. 2b). Each ovicell originates as a minute lamina growing distally from the maternal zooid orifice; this becomes the inner entooecial capsule. Simultaneous changes to the distal zooid or zooids include the obscuring of frontal pseudopores by secondary calcification and the gradual delineation of a circular distal depression (Fig. 3). This area marks the extent of the future ovicell and, later in ontogeny, the edges of the area (which is a frontal extension of the cryptocystal frontal shield of the distal zooids) become increasingly raised and eventually curve over and fuse medially, forming the ectooecium and enclosing the entooecial capsule contributed by the proximal maternal brooding zooid. Suture lines occur where more than one distal zooid has contributed to the ectooecial cover, and the ovicells become sunken as secondary calcification thickens the entire colony frontal. Large, irregular pores in the calcification are 'carried up' from the areolae above the marginal frontal septulae and these, together with the raised mucronate processes, give the colony an appearance unlike that of any other species (Fig. 2b).

Many colonies were collected alive from off Townsville in 1982. These possessed extensive, turgid rhizoid systems. Most of each rhizoid was buried in the muddy sand of the sea bottom, but supported the bilaminar 'head' of feeding zooids several centimetres above the surface of the substratum. The larval behaviour, the settlement and early astogeny of *P. arnoldi* have been described (as *Parmularia* sp.) by Cook & Chimonides (1985).

A small, worn fragment with zooids with similar, elongated orifices (BMNH 1882.2.23.498, Arafura Sea, off the Northern Territory, Australia, 68-72m) may belong to *P. arnoldi*. If con-

firmed by further specimens, this would extend its range across the northern coast of Australia.

ACKNOWLEDGEMENTS

We thank Dr P. Arnold (Museum of Tropical Queensland) and Dr A. Birtles (James Cook University of Northern Queensland) for their help in collecting and maintaining living colonies of *Parmularia*, and Dr J.D.D. Bishop (Port Erin Marine Laboratory, UK) for constructive criticism.

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TWO BIVALVES FROM THE MIDDLE DEVONIAN BURDEKIN FORMATION, NORTH QUEENSLAND

ALEX G. COOK

Cook, A.G. 1993 06 30: Two bivalves from the Middle Devonian Burdekin Formation, north Queensland. *Memoirs of the Queensland Museum* 33(1): 49-53. Brisbane. ISSN 0079-8835.

The bivalves *Phenacocyclas pohli* LaRocque and *Modiomorpha mitchellae* sp.nov. are found within the Burdekin Formation, to the north of Charters Towers, north Queensland. They represent respectively the first lucinid and modiomorph described from these strata. *M. mitchellae* sp.nov. is characterised by its large size and elongate shape. □ *Mollusca, Bivalvia, Lucinidae, fossil, Phenacocyclas, Modiomorpha mitchellae, new species, Queensland, Middle Devonian, Burdekin Formation.*

Alex G. Cook, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 14 August, 1992.

Collections of molluscs from the Middle Devonian (Givetian) Burdekin Formation have yielded two bivalve genera previously unreported from this formation, *Phenacocyclas pohli* LaRocque and *Modiomorpha mitchellae* sp.nov.

Stratigraphic nomenclature for the area is outlined in Wyatt & Jell (1980) and Lang et al. (1990). The Fanning River Group is divided into three formations— the Big Bend Arkose, mostly coarse grained siliciclastics is overlain by the Burdekin Formation, a dominantly limestone sequence, which in turn is overlain by the Cultivation Gully Formation, a predominantly siliciclastic unit. In the Burdekin Downs area (Fig. 1), the location of *Phenacocyclas pohli* LaRocque, the Burdekin Formation is about 90m thick and the Cultivation Gully Formation has been eroded. In the Paynes Lagoon area (Fig. 1), the locality of *Modiomorpha mitchellae* sp.nov., the only manifestation of the Burdekin Formation is a 2 to 5m thick molluscan shell bed that rests unconformably on Precambrian Basement.

In previous investigations of the molluscan fauna, Etheridge (1917) described a single gastropod from the Group and Heidecker (1959) described three gastropods and the two bivalve taxa from the Big Bend area: *Tanaodon louderbacki* Kirk and *Neoactinodonta amygdalina* Heidecker. Both Heidecker's species have been reassigned to *Tanaodon louderbacki* Kirk by Pojeta, Zhang & Yang (1986). Zhen (1990) reviewed the gastropod biofacies found at the base of the Fanning River Group, but did no further taxonomic investigations of the molluscan fauna. Cook (in press) describes a fourth genus of gastropod from the Big Bend Arkose and lower Burdekin Formation.

The Burdekin Formation has been assigned a late Eifelian to Givetian age based on limited conodont data, rugose coral associations, and the presence, in abundance, of *Stringocephalus* sp. No precise zonal ages for the localities given in this work are available but the coral fauna associated with both molluscs suggests a Givetian age (Zhen, 1990).

SYSTEMATIC PALAEONTOLOGY

Phylum MOLLUSCA
Class BIVALVIA Linné, 1758
Subclass HETERODONTA Neumayr, 1884
Order VENEROIDEA Adams and Adams, 1856
Superfamily LUCINICOIDEA Fleming, 1828
Family LUCINIDAE Fleming, 1828

Phenacocyclas LaRocque, 1950

TYPE SPECIES

Phenacocyclas pohli LaRocque by original designation from the Middle Devonian of Michigan.

DIAGNOSIS

Equivalved, irregularly rhomboidal lucinoideans with a prominent posterodorsal radial sulcus, slight anteroventral embayment and comarginal ornament. Hinge is straight and short with small umbones, narrow escutcheon and small lunule. Internal molds with posteroventral notch, two large elongate adductor scars and prominent irregular sigmoidal grooves. Posterior adductor deeper and narrower than anterior scar. Dentition small and poorly known: one probable small lateral tooth and probable small cardinal tooth.

REMARKS

Phenacocyclas, according to LaRocque (1950) is separated from *Paracyclas* Hall by the posterodorsal sulcus, the arrangement of the adductors, the presence of a strong posteroventral notch and

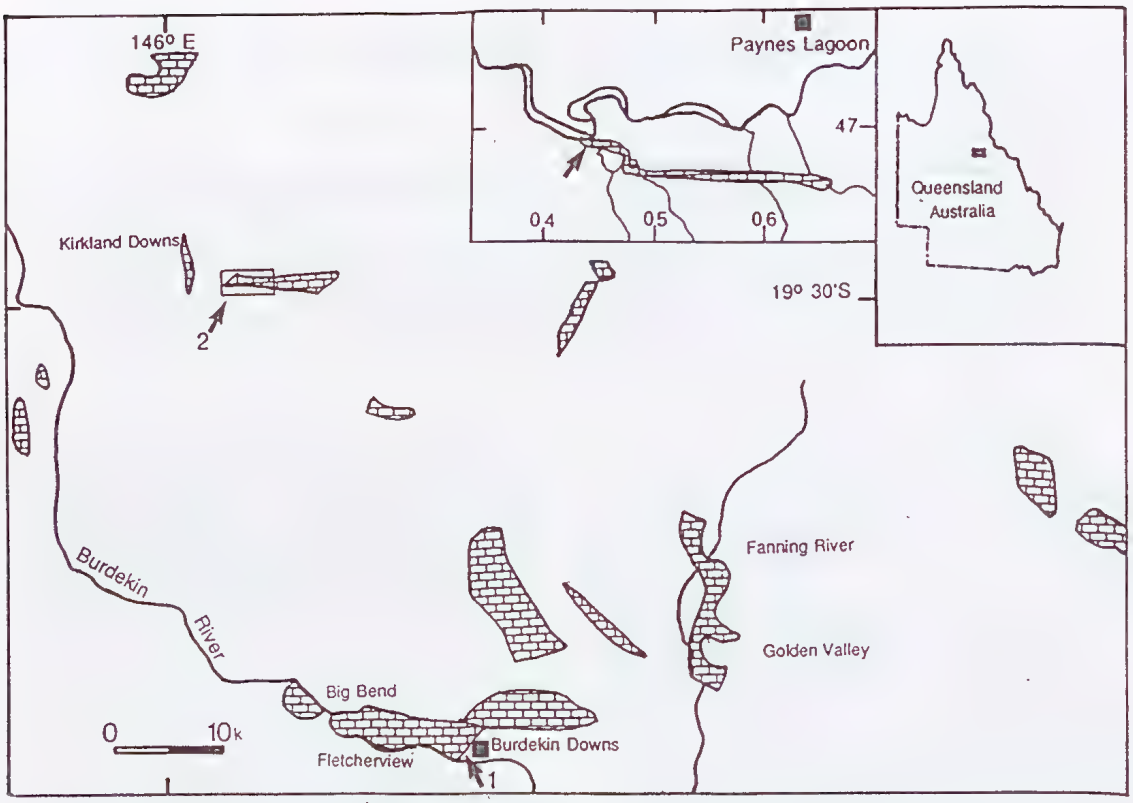

FIG. 1. Outcrop pattern for the Fanning River group within the Townsville Hinterland, showing collection localities (arrows) for *Phenacocylcas pohli* LaRocque (1) and *Modiomorpha mitchellae* sp.nov. (2).

the sigmoidal grooves on internal molds. It differs from *Crassatellopsis* Beushausen and *Montanaria* Spriestersbach on the basis of size of the dentition. The genus has been placed in the Lucinidae by Chavan (1969).

Phenacocyclas pohli LaRocque
(Fig. 2)

Material Examined
Nine conjoined specimens with shell intact and mostly free from host lithology of impure carbonate wackestone. Only 6 of the specimens are sufficiently complete to provide size data (Table 1). Material housed in Queensland Museum: QMF 22528, QMF 22529: James Cook University JCUF 11806-11812.

Age and Occurrence
Present Study: Middle Devonian (Givetian) Burdekin Formation, Fanning River Group. Collected from hill directly behind Burdekin Downs Homestead, NW of Charters Towers, north Queensland. Grid Reference Dotswood: DU 199 011. Middle Devonian Dundee Limestone and Rodgers City Limestone, Michigan, U.S.A.

Description
Medium to large equivalved rhomboidal shells ranging in height from 35-55mm, in length 42-56mm and width 19-25mm. Strong posterodorsal sulcus present. Slight embayment on the anteroventral margin. Thin shelled, with well developed comarginal ornament consisting of fine growth lines overprinted by coarser irregularly spaced rugations. Hinge and internal structures not seen.

Remarks
Burdekin material is only slightly larger than the type material illustrated by LaRocque (1950)

TABLE 1. Morphometric data for specimens of *Phenacocyclas pohli* from the Burdekin Formation. Measurements in mm.

SPECIMEN	HEIGHT	LENGTH	WIDTH
QMF 22528	43	46	24
QMF 22529	39	44	19
JCUF 11806	55	57	25
JCUF 11807	54	56	24
JCUF 11808	46	42	19
JCUF 11810	45	44	19

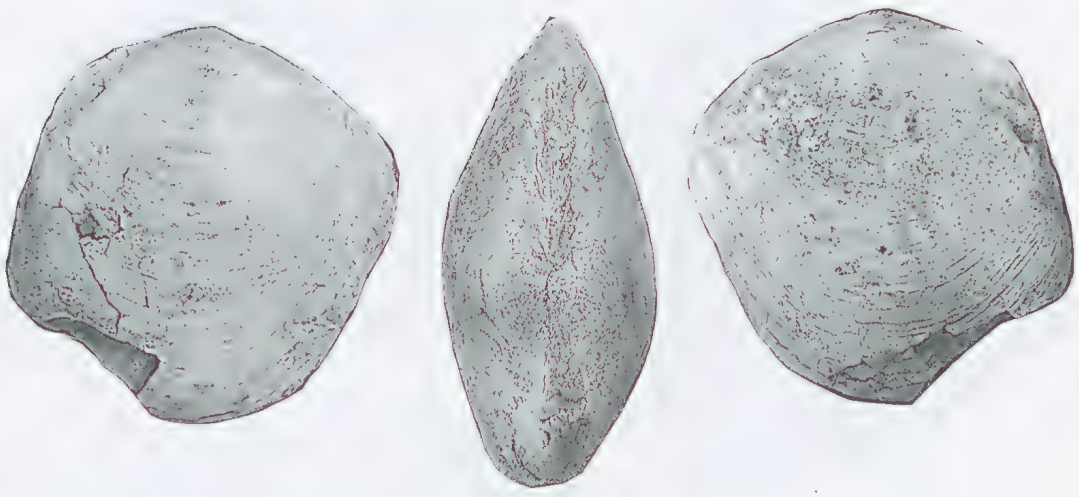

FIG. 2. a-c. *Phenacocyclas pohli* LaRocque JCUF 11806: a, right valve ×0.9; b, left valve ×0.9; c. dorsal view ×1.

and shows all of the external features described for *Phenacocyclas pohli*. Unfortunately the illustrated adult specimens are restricted to internal molds but juvenile material (LaRocque, 1950 pl. 15, figs 1-7) shows features found also in the Burdekin specimens.

Both LaRocque (1950) and Bailey (1983) suggested that *Paracyclas antiqua* (Goldfuss) may belong to *Phenacocyclas*. In particular *Paracyclas antiqua* (Goldfuss) of Beushausen (1895) shows many of the features of *Phenacocyclas*. The size of Beushausen's (1895) specimens, as given by Bailey (1983) is similar to that of *Phenacocyclas pohli* LaRocque. It is possible that the two are synonymous but determination of this awaits detailed examination of type material of *Paracyclas antiqua* (Goldfuss).

Subclass PALAEOHETERODONTA Newell, 1965
Order MODIOMORPHOIDA Newell, 1969
Superfamily MODIOMORPHACEA Miller, 1877
Family MODIOMORPHIDAE Miller, 1877

Modiomorpha Hall & Whitfield, 1869

TYPE SPECIES

Modiomorpha concentrica (Conrad, 1838)

DIAGNOSIS

Modioliform modiomorphids with large wedge-shaped cardinal tooth in left valve, socket in right valve, weak laterals, rugose growth increments.

Modiomorpha mitchellae sp.nov.
(Fig. 3)

MATERIAL EXAMINED

HOLOTYPE: JCUF 11823; internal mold.

PARATYPES: QMF 22684-85: well preserved internal molds, JCUF 11824-28, QMF 22686, 22687.

OCCURRENCE

Middle Devonian (Givetian), north Queensland Australia. Burdekin Formation, Paynes Lagoon Station, 80km W of Townsville.

DIAGNOSIS

Very large, elongate *Modiomorpha* with medium to coarse comarginal ornament.

DESCRIPTION

Large posteriorly elongate shells, modioliform in outline, up to 150mm long. Shell thick, especially anterodorsally, thinning posteroventrally. A break in shell slope, which runs from anterodorsal margin to posteroventral margin on the internal mold, is a weak ridge. Medium to coarse comarginal ornament preserved on JCUF 11824. Invagination along the hinge indicates large cardinal tooth and socket. Hinge plates relatively thick. Anterior adductor scar is small, subcircular. Quick and catch portions are easily discernible. Dorsally adjacent retractor scar is much smaller, subcircular. Posterior scar not preserved.

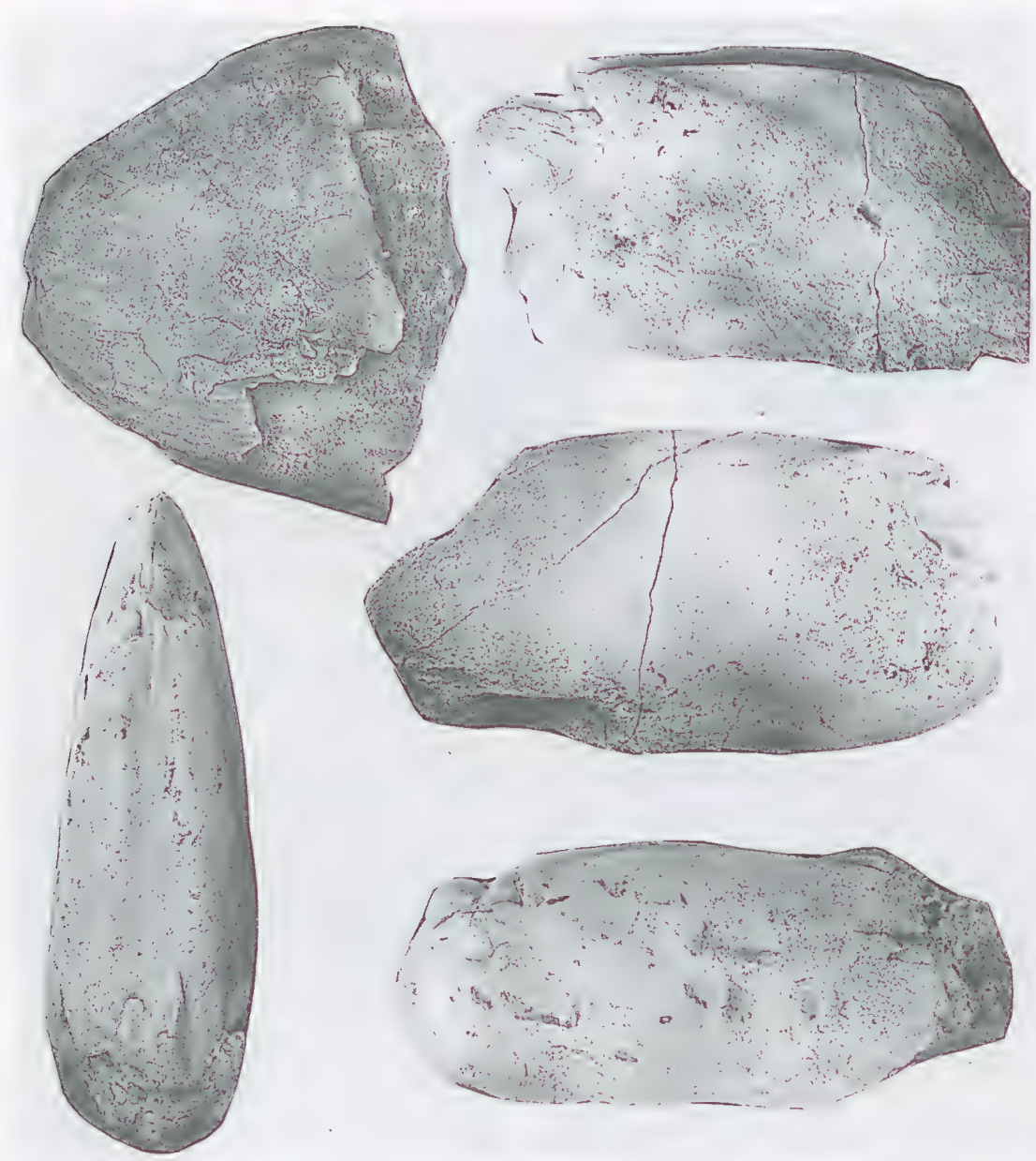

FIG. 3. a-e *Modiomorpha mitchellae* sp.nov: a, Paratype JCUF 11824, external of partial right valve, showing concentric ornament ×1.1; b, Holotype JCUF 11823, internal mold left valve ×1; c, Holotype JCUF 11823, internal mold right valve ×1; d, Paratype QMF 22684, dorsal view of articulated internal mold, showing invagination indicating large cardinal tooth ×1; e, Paratype QMF 22684, internal mold left valve, showing prominent anterior adductor ×1.

REMARKS

The characteristic musculature, dentition, shape and size ally the material to the genus *Modiomorpha*. It is distinguished by its size and rather elongate shape from other species of *Modiomorpha*. *M. concentrica* (Conrad) described by Bailey (1983), Pojeta, Zhang & Yang (1986) and *M. oblonga* Zhang 1977 are smaller despite Pojeta, Zhang & Yang's (1986) comment that *M. oblonga* is of large size. *M. herculi* Bradshaw 1991 (in Bradshaw & McCartin, 1991) is substantially smaller. *M. mytiloides* (Conrad, 1841; in Bailey, 1983) is also a small form. There is some disagreement concerning the systematic

position of *Modiomorpha* Hall & Whitfield. Newell's (1965) scheme is followed here, but Pojeta, Zhang & Yang (1986) express a different view.

ETYMOLOGY

Named for R. L. Mitchell for her contributions to the study of modern mollusca from the Townsville area.

ACKNOWLEDGEMENTS

R. A. Henderson is thanked for endless help and provision of specimens collected by D. H. Wyatt from Paynes Lagoon. JCU Merit grants in 1990 and 1992 contributed to this work, as did the Queensland Museum by the provision of services. M. Wade and P. A. Jell are thanked for their encouragement. The owners of Paynes Lagoon and Burdekin Downs are thanked for their hospitality.

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A RECORD OF THE COMMON PLANIGALE AT MYORA SPRINGS: THE FIRST DASYURID FROM NORTH STRADBROKE ISLAND. *Memoirs of the Queensland Museum 33(1): 54. 1993:-* A Common Planigale (*Planigale maculata*) was captured at Myora Springs (153°25'E, 27°29'S), North Stradbroke Island on February 11, 1993. The animal was trapped during a survey by Griffith University staff and third-year students, conducted as part of a 'field ecology' course. The trapping effort at Myora Springs consisted of four pitfall traps (20 litre buckets c.38cm deep and 30cm diameter), each situated half-way along a 20m drift fence, as well as 40 small Elliott traps, all of which were set over four nights during February 9-12, 1993. The planigale was caught in one of the pitfall traps.

The Myora Springs region lies on the western edge of North Stradbroke Island, where Capembah Creek drains into the ocean. In this area there is a complex mixture of plant communities, including rainforest, *Melaleuca quinquenervia* forest and woodland, sedgeland, eucalypt forest and woodland, and disturbed areas. The habitat in which the traps were set was mapped by Coutts (1992) as partly disturbed closed forest, incorporating patches of simple notophyll vine forest dominated in part by *Melicope elleryana* with *Eucalyptus robusta* emergents and in part by *Callitris columellaris* with *Eucalyptus* spp. emergents; grading on its southern side into an open forest dominated by *Melaleuca quinquenervia* with *Eucalyptus robusta* emergents, and on the eastern side into open forest dominated by *E. pilularis*. The area of closed forest is not much more than one hectare, but is the only area of notophyll vine forest on North Stradbroke Island (Kikkawa, 1975).

The trapped specimen was a young male (testes clearly visible although not very large), of weight 6.0g, head and body length 59mm and tail length 48mm. After being caught it was retained in captivity for three days, during which period it was taken to the Queensland Museum where its identity was confirmed (S. Van Dyck) and it was photographed. It was then released on Stradbroke Island at the point of capture.

This specimen is significant because it is the first record of the family Dasyuridae from North Stradbroke Island. Three dasyurids (*Antechinus flavipes, Sminthopsis murina* and *Planigale maculata*) have been recorded from Fraser Island (Van Dyck, 1991), but none from either North Stradbroke or Moreton Islands, in spite of extensive survey effort on North Stradbroke Island (Martin, 1975; Barry & Campbell, 1977; Van Dyck, 1991). *Planigale maculata* was, however, recorded some time ago (1960) from nearby Russell Island (Van Dyck, 1983).

The present new record may be a consequence of using pitfall traps for sampling. Trapping with baited Elliott traps during the past ten years at Myora Springs during annual Griffith University field excursions (typically with 50-100 traps set over three nights each year) has usually yielded high capture rates of *Melomys* species (*M. burtoni* or *M. cervinipes*), moderate capture rates of *Rattus lutreolus*, and occasional captures of *Isoodon macrourus*. In 1993, *Mus musculus* was also captured in the area for the first time, probably a consequence of recent residential development nearby. Pitfall traps were set for the first time in 1993, and four pitfalls set over four nights caught one *Planigale maculata* and two juvenile *Melomys* sp.

The absence or relative scarcity of dasyurid marsupials on the large sand islands of Moreton Bay is a puzzling biogeographical pattern (see Barry & Campbell, 1977). The lack of dasyurids from these islands cannot be simply a consequence of lack of appropriate sampling, since *Antechinus* spp., if present, should have been caught using conventional baited traps. The distribution of habitat may also be a contributing factor: Stradbroke and Moreton Islands are dominated by 'dry' sclerophyll and heathland communities on soils very low in nutrients (see for example Clifford & Specht, 1979), whereas Fraser Island supports large areas of the moister forest types. Frequent fires on North Stradbroke Island have probably also influenced the habitat available to dasyurids (Martin, 1975). Further pitfall sampling in other parts of North Stradbroke Island would be required to determine whether *P. maculata* occurs throughout the island, or is localised within particular areas such as Myora Springs.

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C.P. Catterall, Faculty of Environmental Sciences, Griffith University, Nathan, Queensland 4111, Australia; 26 February, 1993.

CHERAX CARTALACOOLAH, A NEW SPECIES OF FRESHWATER CRAYFISH (DECAPODA: PARASTACIDAE) FROM NORTHEAST AUSTRALIA

JOHN W. SHORT

Short J.W. 1993 06 30: *Cherax cartalacoolah*, a new species of freshwater crayfish (Decapoda: Parastacidae) from northeast Australia. *Memoirs of the Queensland Museum* **33**(1): 55-59. Brisbane. ISSN 0079-8835.

A new species of freshwater crayfish, *Cherax cartalacoolah*, from eastern Cape York Peninsula, Queensland is described and illustrated. The new species most closely resembles *C. robustus* Riek, 1951, which occurs in similar, sand dune habitats in southeast Queensland, and can be distinguished by the morphology of the carapace and first chelipeds. □ *Crustacea, Parastacidae, Cherax, new species, northeastern Australia, Cape York Peninsula, freshwater, taxonomy, biology.*

John W. Short, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 3 March, 1993.

Australian species of *Cherax* Erichson were last revised by Riek (1969), who listed 27 species. Short (1991) described *C. nucifraga* from the Northern Territory.

Cherax cartalacoolah sp.nov. was brought to my attention in October 1991 by Mr Rolly McKay, Queensland Museum. Only two immature specimens and a number of carapace fragments and chelae were available but this was sufficient to establish that the species was new to science. A Queensland Museum expedition to the Cape Flattery area in November 1992 by Mr Peter Davie and myself, collected further material including mature adult specimens.

Abbreviations used in text: QM, Queensland Museum; CL, postorbital carapace length; T, thoracic sternite, T6, thoracic sternite six etc.

Cherax cartalacoolah sp.nov.
(Figs 1-3, 4A,B)

MATERIAL EXAMINED

HOLOTYPE: QM W18224, ♂ (30.3mm CL), Cape Flattery, second creek south of headland, 14°59.2'S, 145°20.2'E, supralittoral, in burrow amongst rushes fringing lagoon, peaty sand, freshwater, pH 5, hardness 40ppm, water temperature 33°C, dissolved oxygen 1.7ppm, altitude c.10m, 16/11/1992, J. Short, P. Davie.

ALLOTYPE: QM W18225, ♀ (23.6mm CL, right cheliped missing, left damaged at base of pollex), from same burrow as holotype.

PARATYPES: QM W17231, ♀ (14.4mm CL), Arnies Lake, Cape Flattery, 14°58'S, 145°19.5'E, 11/10/1991, R. McKay. QM W17234, ♂ (18.4mm CL), Windmill Lake, Cape Flattery, 14°58'S, 145°17.5'E, 13/09/1991, R. McKay. QM W18223, ♀ (16.2mm CL), Vince's Lake, Cape Flattery, 14°59'S, 145°16'E, supralittoral, burrow in bank of artificial drainage channel, peaty sand, altitude c.15m, 16/11/1992, J. Short, P. Davie. QM W18226, ♂ (13.7mm CL), 1 imm. (7.3mm CL), same locality and physiochemical data as holotype and allotype, in burrows along water line of lagoon. QM W18228, 4♂♂ (12.5-24.9mm CL), ♀ (19.8mm CL), Cape Flattery, 14°59.2'S, 145°18'E, 0.75m, artificial drainage channel, freshwater, peaty sand, water tannin-stained, fringing heathland/rushes, pH 5, hardness 80ppm, 17/11/1992, trapped, J. Short, P. Davie.

COMPARATIVE MATERIAL: *Cherax robustus* Riek, 1951 (from the vicinity of the type locality), QM W15312, 12♂♂ (17.0-30.4mm CL), 5♀♀ (17.9-25.2mm CL), Coomboo Lake, Fraser Is., 25°14'S, 153°10'E, in burrows around periphery of lake, 17/06/1987, S. Brooks, M. Tait.

DESCRIPTION OF HOLOTYPE

Rostrum triangular, dorsally flattened, slightly recurved distally, punctate proximally, glabrous to base of acumen; length c.1.3 × breadth (1.6-2.3 in allotype/paratypes), reaching penultimate segment of antennular peduncle (terminal segment in small paratypes); with moderately-developed lateral carinae, carinae commencing in line with postorbital processes, terminated at base of acumen by blunt process (spinate in several paratypes, particularly smaller specimens); ventrolateral margins setose; acumen blunt (acute in allotype/paratypes), setose.

Eyes with cornea large, globular, well pigmented, eyestalks slightly concealed by rostrum. Antennula without unique features. Scaphocerite short, length c.1.9×breadth (2.0-2.4 in allotype/paratypes), reaching end of rostrum (slightly exceeding rostrum in allotype/paratypes), broad-

est at mid-length; lamina broadly rounded mesially, lateral margin terminating in well developed spine. Antennal peduncle setose ventrally, coxocerite acute anteriorly (spinate in allotype/paratypes), basicerite laterally spinate.

Carapace punctate, breadth c.0.6×CL, depth c.0.6 × CL; postorbital carinae poorly developed, excavated with interconnected punctations, forming irregular sulcus, armed with blunt process anteriorly (spinate in allotype/paratypes), diverging posteriorly, length c.1/3 cephalon length; cephalon with few tubercles ventrally (absent in small paratypes); branchiostegites slightly inflated, with few indistinct tubercles along cervical groove (spines on allotype/paratypes), granulose anteriorly (non-granulose in smaller paratypes); branchiocardiac grooves distinct (indistinct or absent in paratypes).

FIG.1. *Cherax cartalacoolah* sp.nov., holotype ♂ (30.3mm CL), QM W18224, dorsal view.

FIG.2. *Cherax cartalacoolah* sp.nov., holotype ♂ (30.3mm CL), QM W18224, ventral view.

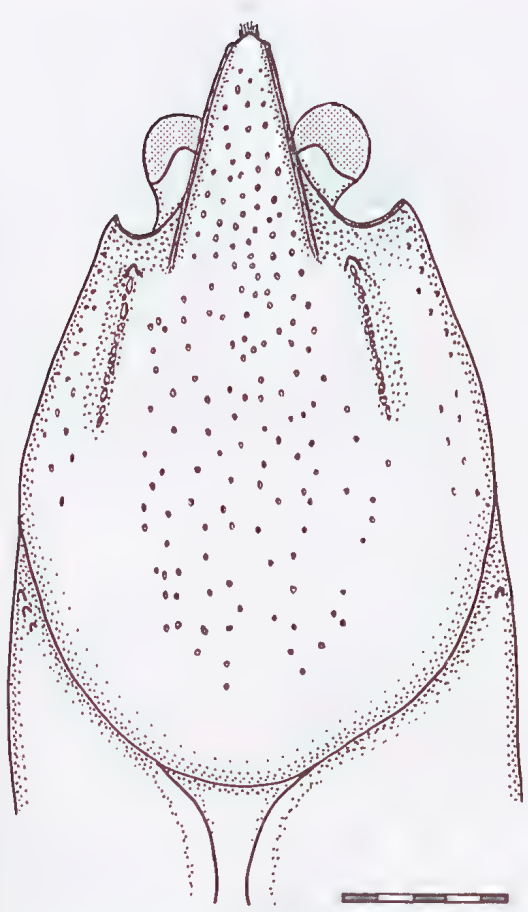

FIG.3. *Cherax cartalacoolah* sp.nov., holotype ♂, QM W18224, anterior carapace and rostrum. Scale divisions in mm.

Epistome slightly concave, sparsely setose, without obvious tubercles, lateral margins entire, slightly crenulate. Mouthparts without unique features. Branchial formula typical for genus (cf. Holthuis, 1949), with posterior arthrobranch above fourth pereiopod reduced.

First chelipeds large, subequal (isomorphic in paratypes), distal merus reaching end of scaphocerite (carpus in allotype/paratypes); outer margin of chelae moderately convex; fingers without obvious gape, opposing edges densely setose, bearing low rounded teeth; pollex broad basally; dactylus equal to manus in length; manus moderately broad, breadth equal to length (less than length in paratypes), dorsum moderately-convex longitudinally (slightly convex in allotype/paratypes), strongly convex laterally, mesial margin serrations restricted to proximal half; carpus c.0.3 chela length, bearing large, uncinate mesial spine, blunt process at anteroventral condyle (acute in paratypes), similar process at ventromesial angle followed by two or three tubercles posteromesially, anteromesial angle with dense pubescence of long setae; merus of typical shape, c.0.6 chela length, dorsal carina armed with blunt process (spinate in allotype/paratypes) followed by series of tubercles, ventral surface with pubescence of setae and numerous strong cuticular processes, two or three larger than rest (spinate in allotype/paratypes).

Sternal keel sharp, without spines, lateral processes juxtaposed on T7 and T8, bearing conspicuous pores on T6 and T7. Abdomen punctate, somite 2 pleurae with deep concavity.

COLOURATION

Body colour varying from rusty brown to bluish-grey, ventral manus of first chelipeds magenta to cyanine blue, articular membrane between merus and carpus geranium red.

BIOLOGY

Freshwater, fossorial, burrows terminating slightly below level of water table, supralittoral to shallow littoral areas around perch lakes and along creek banks. Collected from low altitude <15m, peaty sand areas within sand dune formations, generally amongst rushes, fringing heathland. Recorded physiochemical tolerances: pH 5, hardness 40-80ppm, water temperature 33°C, dissolved oxygen 1.7ppm.

DISTRIBUTION

Cape Flattery, northeast Queensland. It is likely, with further collecting, that the range of this species will be extended into other sand dune areas between Cape Bedford and Lookout Point.

ETYMOLOGY

An aboriginal word meaning 'a water hole between two sandhills' (cf. Reed, 1970), which is an accurate description of the type locality. The specific name is to be treated as a noun in apposition.

SYSTEMATIC POSITION

The new species most closely resembles *C. robustus* Riek, 1951, from southeast Queensland, which also occurs in acidic, peaty-sand habitats and has similar colouration. The following morphological features can be used to distinguish the two species:

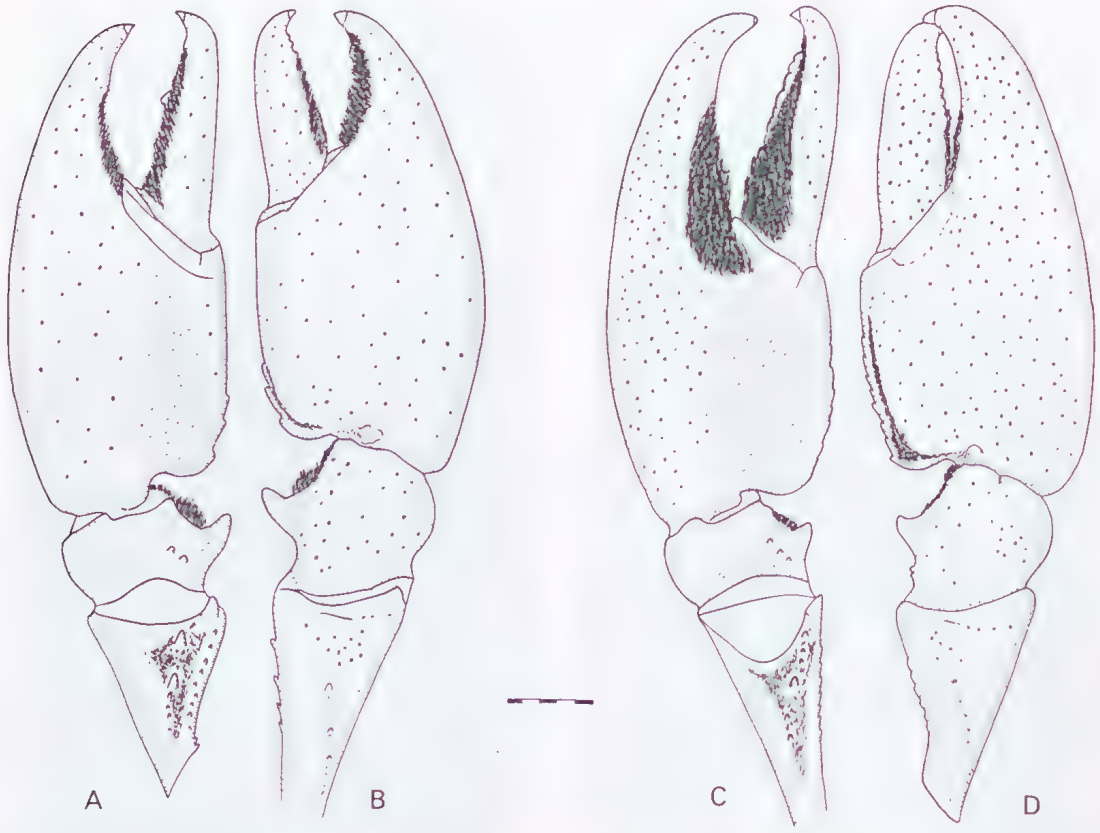

FIG.4. *Cherax cartalacoolah* sp.nov., holotype ♂, QM W18224: A, ventral view of right first cheliped; B, dorsal view of right first cheliped. *Cherax robustus* Riek, 1951, ♂ (30.2mm CL), QM W15312: C, ventral view of right cheliped; D, dorsal view of right cheliped. Scale divisions in mm.

1. The mesial carpal spine on the first chelipeds is much stouter in *C. robustus* and is usually followed by one or more tubercles. In the present species there are no tubercles behind the spine.

2. The ventral setation on the pollex of the first chelipeds continues for some distance onto the manus in *C. robustus*. In the present species the setation is restricted to the opposing edge of the pollex and does not continue onto the manus.

3. The mesial serrations on the manus of the first chelae continue over about two thirds of the mesial margin length in *C. robustus* whereas in the present species they are restricted to the proximal half.

4. Large adults of the new species have well-developed, branchiocardiac grooves which are lacking in *C. robustus*.

5. The punctations along the postorbital carinae form an irregular sulcus in the present species. In *C. robustus* the punctations sometimes connect anteriorly, but are otherwise well separated.

C. cartalacoolah can easily be separated from nominal species of the *'depressus'* group (sensu Riek 1969), which also occur east of the Great Dividing Range in northeast Queensland, by the presence of setal pubescences on the mesial carpus and ventral merus of the first chelipeds.

C. rhynchotus Riek, 1951, which occurs in similar habitats to the new species on northern Cape York Peninsula and Badu Is., Torres Strait, is not a closely allied species and belongs instead to the *'quadricarinatus'* species-group (cf. Short, 1991).

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Cape Flattery Silica Mines Pty Ltd and the Hopevale Aboriginal Community preceding the 1992 collecting trip to Cape Flattery. I am also indebted to John Benfield, Cape Flattery Silica Mines Pty Ltd, for the use of facilities and the assistance of his staff. In particular, Paul Miller provided support and local knowledge during the collecting effort. Mr Steve Brooks donated specimens of *C. robustus* to the QM. Jeffery Wright printed the photographs.

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A RECORD OF COMMUNAL EGG-LAYING IN THE SKINK *CARLIA TETRADACTYLA*. *Memoirs of the Queensland Museum 33: 60. 1993:-* During a visit to the Oakey area, southeast Queensland on 25 November 1992, a communal nest of 25 skink eggs was located. The site — a disused railway line — was approximately 8km NW of Oakey township and consisted of a relatively continuous row of wooden sleepers.

The nest was located beneath a single sleeper, which was lying on an approximate north-south axis, at its northern end. The whole sleeper was also angled slightly to the west. The eggs varied little in size. All were partially buried in the soil. The eggs were not measured at the time, but their size suggested they could belong to *Carlia tetradactyla*, a very common species at the site. Considering the paucity of records of communal nesting for *Carlia*, one egg was retained by one of us (RP) for artificial incubation to confirm its identification.

On return to Brisbane the egg was transferred to a small plastic container with a little soil from beneath the sleeper and sprayed lightly with water. Access to an incubator was not possible immediately, so the container was maintained between 25-30°C near a 60 watt incandescent light bulb. After two days, the egg had shrivelled markedly and the upper surface had turned a tea-brown colour. However, after a liberal spraying, it almost regained its original shape, though some small wrinkles remained until hatching. After five days the egg was placed in an incubator maintained at 29.5-30.5°C.

On the 3 December 1992, the container was removed from the incubator for the purpose of taking measurements of the egg. However, on opening, it was found the egg had already hatched. Even so, approximate measurements were taken of the empty egg-shell (15.8 × 10mm). The hatchling was tentatively identified as *C. tetradactyla* and a snout-vent measurement was taken (27.6mm). It was then transferred to a small holding container where it thrived and began feeding on hatchling locusts within 4-5 days. The specimen was later taken to the Queensland Museum, where its identification was confirmed (P. Couper). It was subsequently lodged as Queensland Museum specimen number J56882.

Considering the consistent clutch size of two eggs for *C. tetradactyla* (Greer, 1989), the large number of eggs found by us indicates the use of the nesting site by some 13 individual females (or a smaller number of animals laying multiple clutches). Greer states that the communal nests of two genera, *Lampropholis* and *Saproscincus*, usually contain eggs laid almost simultaneously, or at least within a few of hours. He also notes that (at least with the above two genera) nests always consist of eggs from only one species. Thus it seems fair to assume that all 25 eggs belong to *C. tetradactyla*, especially as there were no other abundant, similarly-sized species observed in the vicinity.

Greer (1989) cites only one reference (Wilhoft, 1963) for communal nesting in the genus *Carlia*, *C. rhomboidalis* (= *C. rubrigularis* Ingram & Covacevich, 1989). Thus our record is the second instance of such behaviour in *Carlia*.

It is not known what stimulates several female lizards to lay in the same site. At the nest discovered by us, there did not appear to be any old shells to indicate past use as a favoured nesting site. It is also interesting to speculate why this particular sleeper was chosen amongst hundreds of others. Perhaps it had special features attractive to gravid females, or it may simply have been a choice by one female that, in turn, stimulated several others to lay, possibly by some olfactory cue.

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Robert Porter, Lone Pine Koala Sanctuary, Jesmond Road, Fig Tree Pocket, Queensland 4069, Australia; Grant Husband, Australian Reptile Park, PO Box 192, Gosford, New South Wale 2250, Australia; present address, Territory Wildlife Park, PO Box 771, Palmerston, Northern Territory 0831, Australia; 20 April, 1993.

OCEANAPIA SAGITTARIA FROM THE GULF OF THAILAND

JOHN N.A. HOOPER, MICHELLE KELLY-BORGES AND MARTIN RIDDLE

Hooper, J.N.A., Kelly-Borges, M. & Riddle, M. 1993 06 30: *Oceanapia sagittaria* from the gulf of Thailand. *Memoirs of the Queensland Museum* **33**(1): 61-72. Brisbane. ISSN 0079-8835.

Oceanapia sagittaria (Sollas) is redescribed from shallow water, soft benthic communities surrounding the limestone islands of Ko Samui, southwest Gulf of Thailand, with additional new records from southern Papua New Guinea. Morphological redescription is based on live material, highlighting in particular a unique, tentacle-like, dendritic series of exhalant canals with its complex of oscules on the apex of the primary (open) fistule. Evidence is presented to suggest that this capitate structure serves as both a complex series of exhalant pores and canals, and an asexual dispersal propagule. Scanning electron microscope studies also detected an additional morphology of toxa microscleres, not previously recorded for the species, and studies of skeletal structure indicate that the species is more appropriately included in the family Oceanapiidae (Porifera, Demospongiae, Haplosclerida), being the sixth member of the 'biminia' group of *Oceanapia* species. The distribution and comparative morphology of this species group are discussed. □ *Oceanapia sagittaria, Porifera, Demospongiae, Haplosclerida, Oceanapiidae, Gulf of Thailand, oscular structure, asexual propagule, taxonomy.*

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Species of *Oceanapia* are common, with more than 50 nominal species recorded for the Indo-west Pacific region alone, relatively abundant in both soft and hard substrates, and widely distributed (known throughout the world's oceans: Antarctic, amphi-Atlantic, Mediterranean, Red Sea, western and eastern Indian Ocean, Indo-Malay archipelago, Indo-west Pacific, Japan, New Zealand and eastern Pacific Ocean). However, many of these species are poorly known: most *Oceanapia* species have been described only from preserved material; in many cases they have been described only once; in several instances species descriptions are based solely on incomplete individuals (e.g. fistules); and in some cases species were created on the basis of only minor differences in spicule morphometrics from their siblings. These problems are common to many groups of sponges, but possibly they are most apparent in the relatively morphologically depauperate Haplosclerida, including *Oceanapia*. Whilst reexamination of the type material for many of these species is usually necessary (the original descriptions being very brief and/or very poor), generally this process does no more than confirm or refute those characters already described for the species. Consequently, *Oceanapia* appears to contain many species differing from each other only slightly in any of their major characters (growth form, spicule morphology, spicule size, skeletal structure), whereas in situ observations of live populations are much more informative in discriminating sibling species. In this present paper we redescribe *Oceanapia sagittaria* (Sollas) from live populations in the Gulf of Thailand, including in situ observations of intact capitate, oscular structures peculiar to this species, whereas the species had previously been described only from preserved material (Sollas, 1902; Burton, 1934; Bergquist, 1965), virtually all fragmented. We also describe some observations of populations from southern Papua New Guinea.

METHODS

Preparation of material for light microscopy and scanning electron microscopy (SEM) is described elsewhere (Hooper, 1991). The descriptive language system DELTA was used to prepare the taxonomic description (Dalwitz & Paine, 1986). Abbreviations used in the text are as follows: BMNH, Natural History Museum, London; NCI Q66C-, US National Cancer Institute shal-

low water collection program (Australian Institute of Marine Science, Townsville, contract) – primary material now in Smithsonian Institution, NTM and QM; NMV, Museum of Victoria, Melbourne; NTM, Northern Territory Museum, Darwin; PMBC, Phuket Marine Biology Center, Phuket, Thailand; QM, Queensland Museum, Brisbane; ZMA, Zoological Museum, Amsterdam.

SYSTEMATICS

Family OCEANAPIIDAE van Soest
Oceanapia Norman, 1869

Oceanapia Norman, 1869 [type species: *Desmacidon jeffreysii* Bowerbank, 1866 (= *D. robusta* Bowerbank, 1866 (Carter, 1882))].
Rhizochalina Schmidt, 1870 [type species: *Rhizochalina oleracea* Schmidt, 1870].
Phloeodictyon Carter, 1882 [type species: *Phloeodictyon isodictyiforme* Carter, 1882].
Biminia Wiedenmayer, 1977 [type species: *Oceanapia toxophila* Dendy, 1922].

Diagnosis

Haplosclerida, predominantly fistulose, with a unispicular, tangential, subisotropic ectosomal skeleton, often detachable, and an irregular, longitudinal and/or transverse system of multispicular tracts with a subisotropic reticulation of single spicules dispersed between forming the choanosomal skeleton; microscleres may include sigmas and toxas (modified from de Weerdt, 1985).

Remarks

The genus, its contents, generic synonymy and relationships with other oceanapiids have been discussed at length by several contemporary authors (Bergquist & Warne, 1980; van Soest, 1980; de Weerdt, 1985; Wiedenmayer, 1989; Fromont, 1991). The synonymy cited above is now generally accepted, although de Weerdt and van Soest (1986) also note that *Rhizochalina* and *Oceanapia* s.s. could be considered two 'convenient' subgenera, differentiated by their consistency and development of their spongin fibre skeletons; the first having strongly developed spongin fibres and the second with a pulpy choanosomal skeleton. However, these apparent differences are not clear-cut for all species (i.e. several species in both nominal genera have intermediate character states), and formal recognition of these 'convenient' subgenera may not be fully justified. In fact, there is equal justification for recognising alternative 'convenient' subgenera within *Oceanapia*, based on microsclere diversity for example (e.g. *Biminia* with toxas and sigmas, *Oceanapia* (s.s.) with only sigmas, and *Phloeodictyon* (s.s.) without microscleres), but this system also lacks a sound phylogenetic basis (de Weerdt and van Soest, 1986).

Oceanapia sagittaria (Sollas)
(Figs 1-20)

Gellius sagittarius Sollas, 1902: 212, pl.15, fig.7.
Adocia sagittaria; Burton, 1934: 538.
Orina sagittaria; Bergquist, 1965: 155-157, figs 18a-c.

Material Examined

NTM Z3679, QM G301346, QM G300640, PMBC 9210: E side of northern island, Ko Wao Yai Group Marine National Park, NW of Ko Samui, S Gulf of Thailand, 9°47.0'N, 99°41.0'E, 6 June 1990, 12.5m depth, coll. M. Riddle, S. Sorokin, J.N.A. Hooper, SCUBA (stn JH-90-016). Unregistered material: Motupore I., southern Papua New Guinea, various dates 1987, coll. M. Kelly-Borges.

Distribution, Substrate and Depth Range

This species is only recorded from Kepulauan Bidang, north of Penang, Andaman Sea (Sollas, 1902), Ko Samui, southern Gulf of Thailand and Motupore Island, southern Papua New Guinea (present study), Koror I., Palau Islands, central western Pacific (Bergquist, 1965), and the Low Isles, Great Barrier Reef (Burton, 1934). It is probably a widely distributed Indo-Malay species, but because of its small, relatively cryptic, burrowing habit the extent of its distribution is still not fully known. The recorded depth distribution is from shallow subtidal waters to approximately 14m. The Thailand collection site – located 50m from shore, at 12m depth on sand and coral rubble slope, rising to coral dominated slope and *Porites* heads, at base of limestone cliffs rising to greater than 70m altitude – contained a population of this species with many specimens, although the species was not seen in any other sites in this region. In southern Papua New Guinea the species is also relatively abundant, found in muddy silt substrates.

Description

Shape. Sponge burrowing into soft sediments; slightly enlarged basal root submerged completely below substrate, with one or more fistules protruding above surface (Fig.1). Basal root (or 'body' of sponge) expanded, bulbous, subspheri-

FIG. 1. *Oceanapia sagittaria* (specimen NTM Z3679) in situ (photo M.Riddle).

cal, more-or-less solid, attached to detritus in soft sediments (Fig. 6). All collected specimens consisted only of single primary fistules, with or without smaller, vestigial, secondary (blind) fistules, erect on single basal roots; primary fistule cylindrical, tubular, hollow, with cavernous central lumen, widest at base, tapering to constriction below apex; fistules simple-flagelliform, flexible, fleshy, mucous-covered in life, although more fragile, thin-walled when preserved. Apex of primary fistule with unusual capitate structure (= capitum), which in life is extremely fragile, subspherical, membraneous on its exterior surface, completely translucent, clearly showing dendritic fibre and canal system within (Fig. 1); membraneous capitum collapses upon collection, leaving only dendritic fibres and spicule tracts, tapering at their ends (Figs 7,8). Dimensions: basal root 11-23mm diameter; primary (open) fistule 33-54mm long, 2-4.5mm external diameter, 1.5-4.0mm internal diameter; secondary (blind) fistules 8-18mm long, up to 2.5mm external diameter; capitum (in life, when intact) approximately 20mm diameter, when preserved (i.e. dendritic fibres situated on apex of fistule) 7-11mm long, 4-10mm wide. Growth form consistent for all known specimens.

Colour. Live colouration of basal root dark brown or black; fistules dark red-brown (Munsell 5R 4/10); fibre bundles inside translucent capitum pale red in life (2.5R 6/10) (Fig. 1). Live colouration relatively consistent. Colour of specimens in ethanol grey-brown.

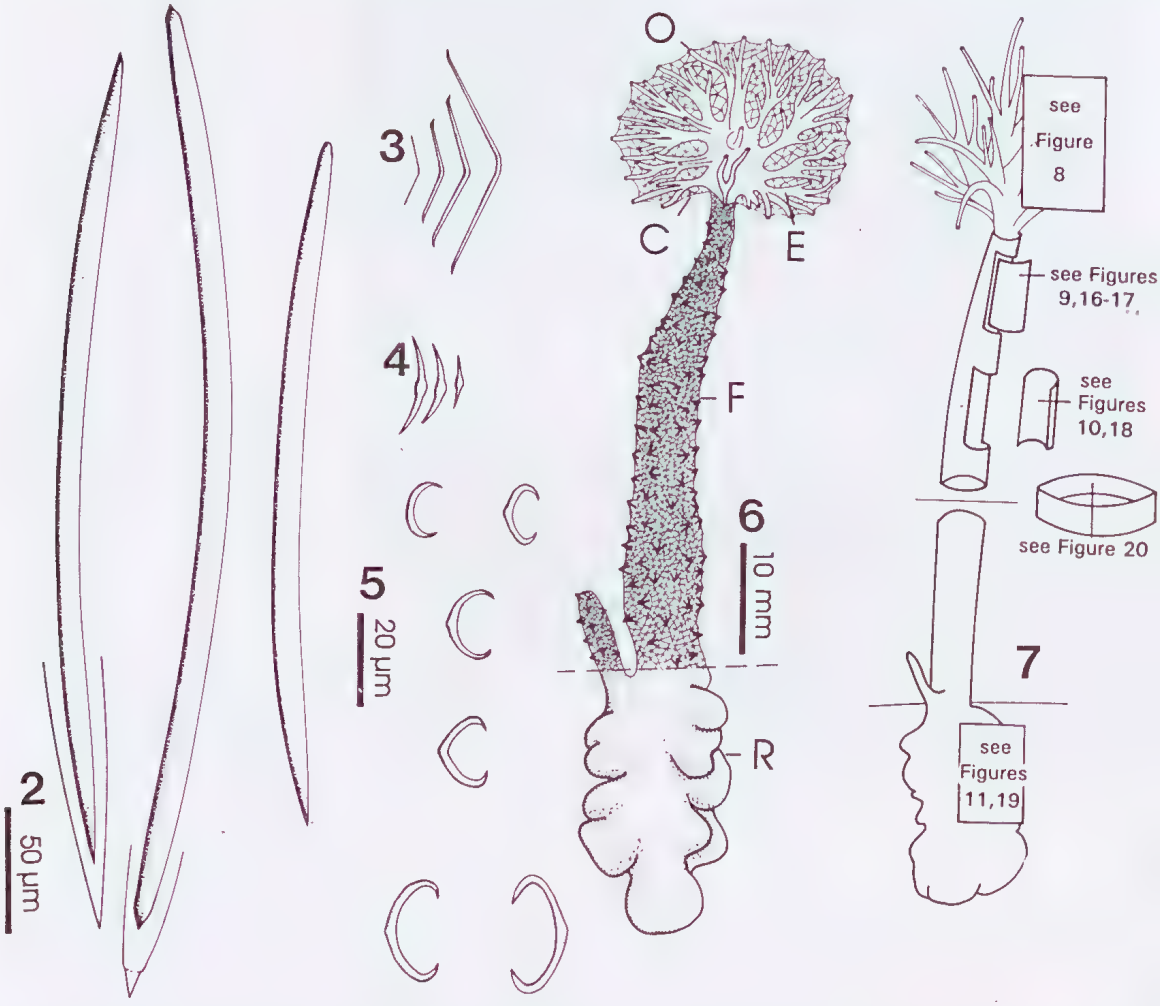
Oscules. Oscules confined to distinct areas on membraneous capitum at apex of sponge; terminal, situated at the ends of dendritic fibre bundles (which probably surround/support exhalant canals), protruding from apex of sponge (Fig. 6); primary fibre bundles thickest at centre of capitum, bifurcating only once or twice within membraneous capitum, with each exhalant canal slightly swollen at apex, and each bearing a single oscule; oscules more-or-less evenly distributed

over entire capitum, minute, 0.2-0.5mm diameter, but not observable in preserved material (i.e. capitum collapses). Inhalant pores not seen.

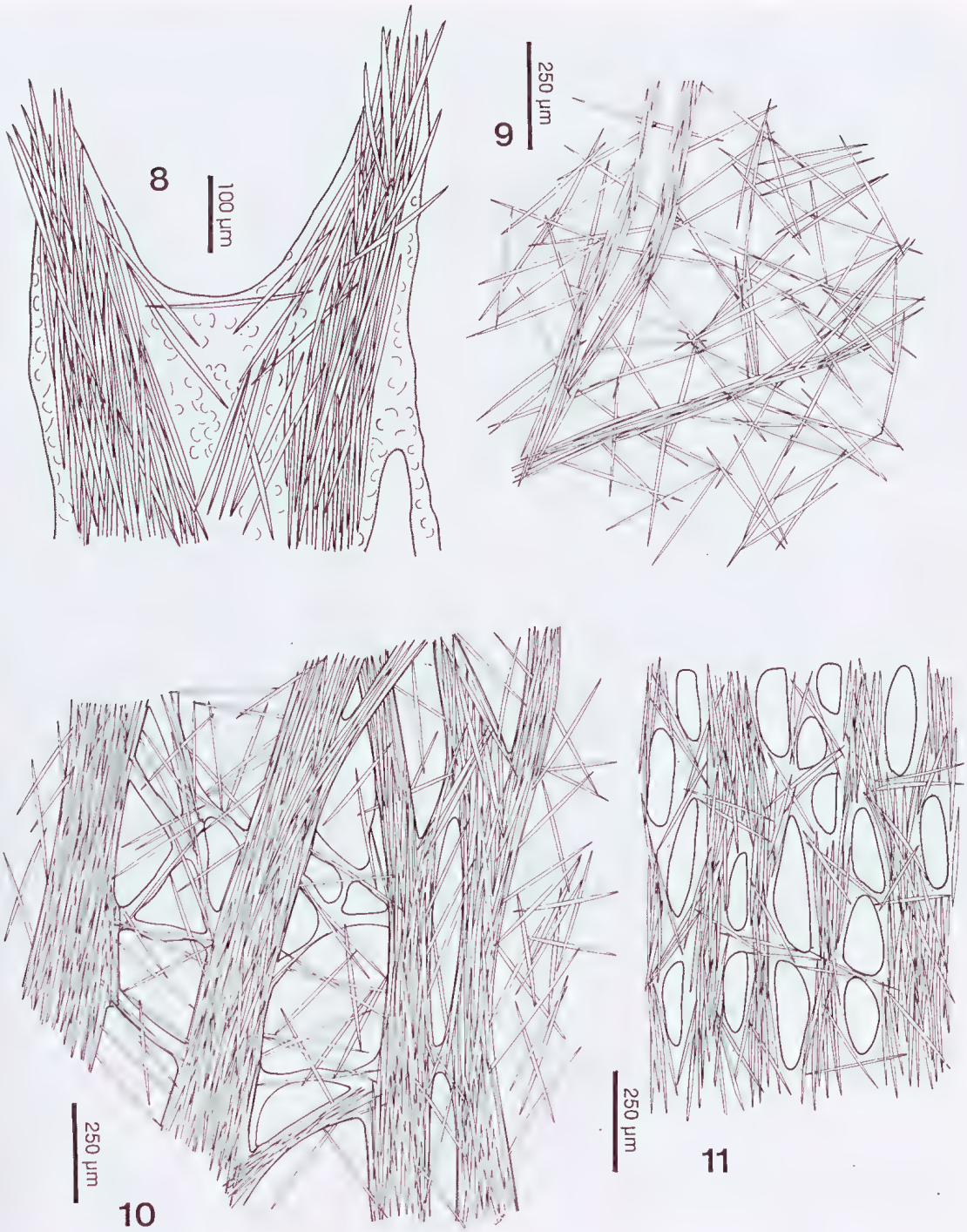
Texture. Fistule soft, elastic, flexible, fragile, easily torn both in life and when preserved; basal root solid, woody, inflexible, easily crumbled.

Surface characteristics. Fistule fleshy, collagenous, pigmented, microconulose, prominently sculptured in life (Fig. 6), with prominent tangential spicule skeleton forming a microscopic, triangular, cobweb-like network (Figs 9,16-17), although appearing more shaggy when preserved. Membraneous capitum skin-like, glabrous in life, with faint, fragile, irregularly isodictyal, tangential spicule skeleton; capitum is translucent in life and choanosomal fibres clearly visible through membraneous surface. Basal root dense, spiculose, heavily pigmented, with smooth surface, and loose, irregular, tangential spicule skeleton, although the latter is not a prominent feature.

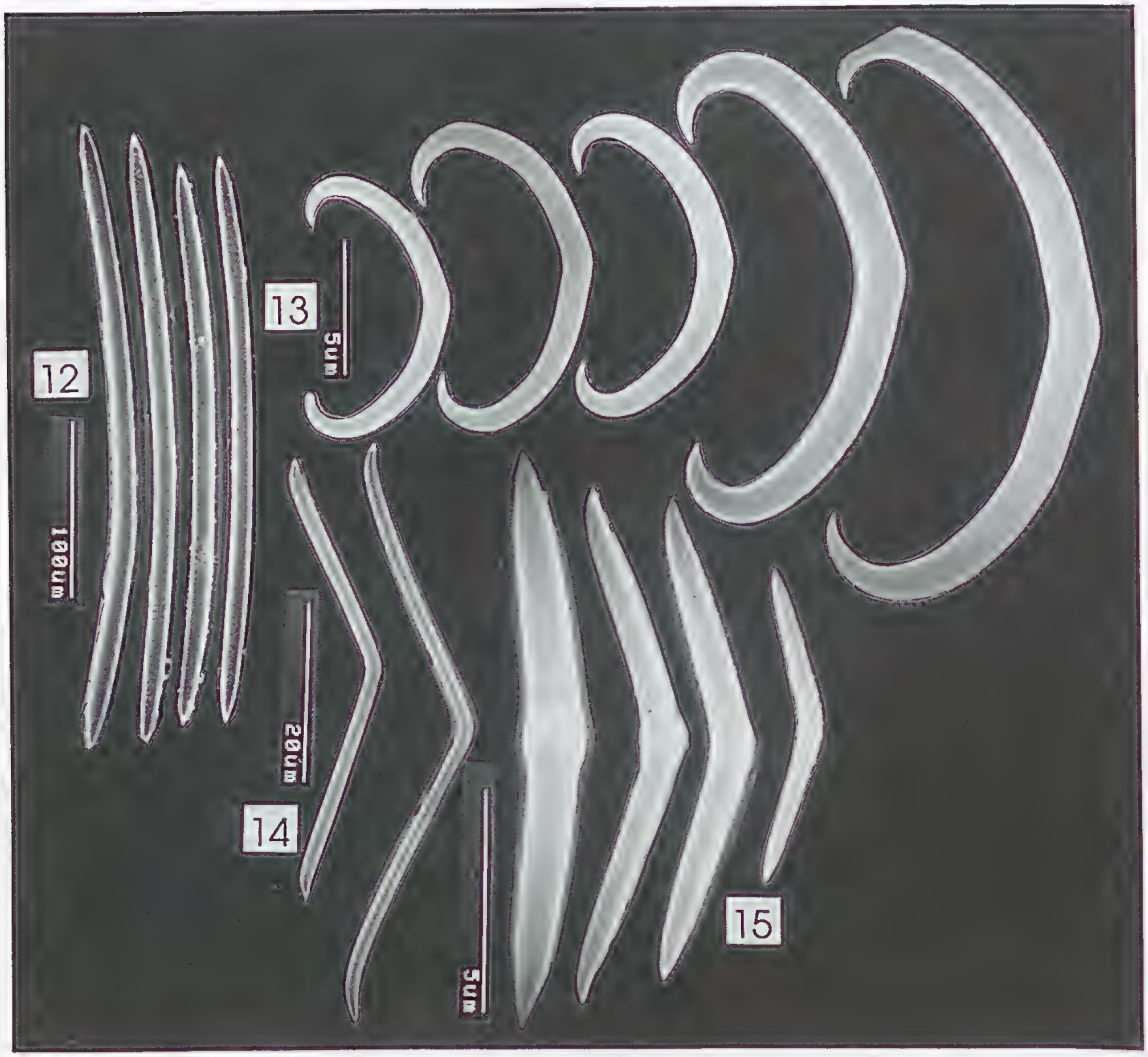
Ectosome and subectosome. Ectosomal skeleton with both unispicular and paucispicular tangential tracts of oxeas (Figs 9,17). Capitum, when intact, with unispicular, subisodictyal, tangential ectosomal tracts, without any support underlying



FIGS 2-7. *Oceanapia sagittaria*, spiculation and morphology. 2, oxeas (and rare anisoxeas). 3, long toxas. 4, robust, centrangulate toxas. 5, centrangulate sigmas. 6-7, interpretation of live, whole specimen (from Fig.1), with stippled basal region indicated below substrate. 7, guide to location of sections depicted in figures 8-20. F=tubular fistule, C=membraneous capitum, R=basal root, with woody exterior and pulpy interior, O=oscule, E=exhalant canal.



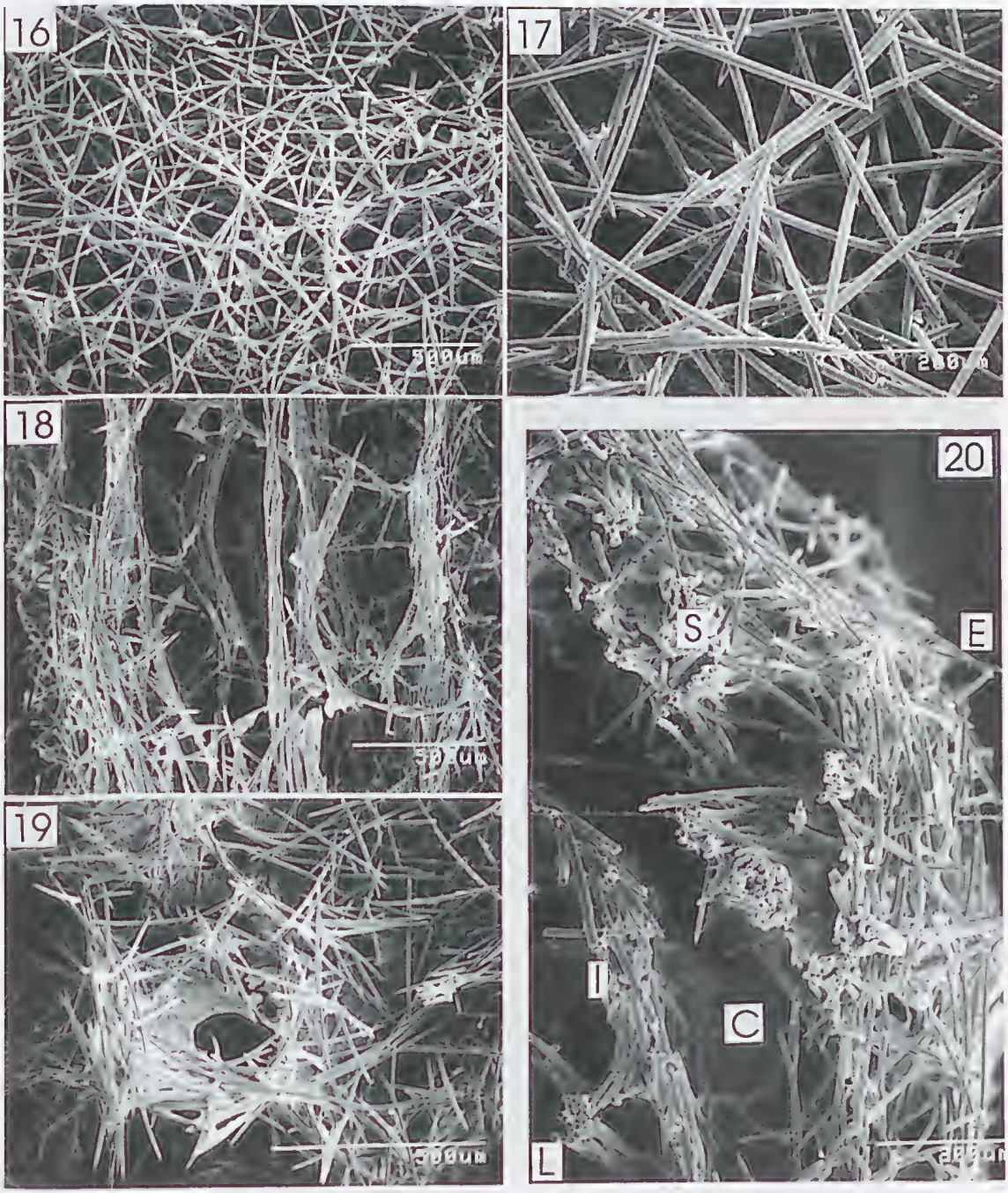
FIGS 8-11. *Oceanapia sagittaria*, interpretation of regional skeletal structures. 8, tip of capitum in preserved condition, showing ascending spicule bundles supporting individual exhalant canals (oscules collapsed). 9, external wall of fistule, showing unispicular, isotropic overlying skeleton and multispicular supporting tracts of subectosome. 10, internal wall of fistule, showing multispicular choanosomal tracts, interdispersed with unispicular, isotropic spicules. 11, section through basal root (or 'body' of sponge, burrowing into substrate), with reticulate, pulpy architecture.



FIGS 12-15. *Oceanapia sagittaria*, scanning electron micrographs of spicules. 12, oxeas. 13, centrangulate sigmas. 14, long toxas. 15, robust, centrangulate toxas.

ectosomal skeleton (unlike most other parts of the skeleton). Fistule with both uni- and paucispicular tracts of oxeas tangential to surface, with multispicular tracts visible just below surface (Fig. 9), and a prominent cavernous area between ectosomal (unispicular and paucispicular) and choanosomal (multispicular) regions (Fig. 20). Basal root with dense, disorganised, unispicular, tangential tracts and dense, multispicular, tracts below the ectosome (Fig. 19), both close to surface. Extra-fibre spicules (i.e. those not associated with the tangential unispicular ectosomal or multispicular subectosomal skeletons) lie in sparse, single or paucispicular subisodictyal tracts throughout the skeleton (Fig. 10).

Choanosome. Choanosomal skeletal structure reticulate, composed of relatively homogenous, dense spicule tracts differentiated into primary (longitudinal) and secondary (transverse) skeletal lines. Primary tracts long, multispicular, 70-160μm diameter, joined by shorter pauci- or multispicular secondary tracts, 30-50μm diameter, together forming irregular elongate or eliptical meshes, 450-1500μm long, 120-250μm wide. Extra-fibre spicules scattered between choanosomal meshes, in unispicular, subisodictyal tracts. Basal root ('body' of sponge), pulpy, occupying most of 'body' diameter, with central lumen of fistules extending several millimetres into 'body', and with large, cavernous meshes pro-



FIGS 16-20. *Oceanapia sagittaria*, scanning electron micrographs of skeletal structure (see Fig. 7 for location of sections). 16, tangential, unispicular, isotropic reticulation of ectosome, exterior wall of fistule. 17, close-up of same. 18, multispicular, mostly longitudinal reticulation of interior wall of fistule. 19, cavernous, pulpy choanosomal skeleton of basal root ('body' of sponge). 20, cross-section through fistule wall, showing exterior unispicular tracts (E), with subectosomal support (S), a cavernous region in between (C), interior multispicular tracts of choanosome (I) lining lumen of fistule (L).

duced by reticulation of longitudinal and transverse skeletal tracts, up to 0.5mm diameter (Figs 11,19). Fistules with greatly compressed choanosomal skeleton, attached directly to the interior of fistule walls (Figs 10,18). Spongin fibre skeleton greatly reduced; spongin fibres typically very light (Figs 10,11), whereas spicules between major tracts (i.e. forming the subisodictyal skeleton) usually bound together by sparse, granular, lightly pigmented collagen. Collagen in mesohyl abundant, darkly pigmented, dispersed evenly throughout, slightly granular, packed with microscleres. Choanocyte chambers minute, ovoid, 12-26μm diameter, lined by sigma and toxa microscleres.

Megascleres. Relatively long, thin, smooth oxeas (Figs 2,12), slightly curved, with fusiform points or occasionally slightly constricted near apex and bearing a sharp, mucronate, abrupt point; very homogenous in size throughout skeleton (length 329-363.4-393μm; width 9-10.8-12μm).

Microscleres. Two categories of microscleres present, both very abundant. C-sigmas (Figs 5,13), of a single size class, varying only slightly in size, usually very small, thin, typically centrangulate, never s-shaped or contort, completely smooth (length 8-12.6-22μm, width 0.5-1.2-2μm).

Toxas include two morphs, the larger more common: (i) long, thin, v-shaped toxas (Figs 3,14), with wide angular central curvature, and reflexed points (at extremities only) (length 28-41.9-68μm; width 0.5-1.2-2.5μm); (ii) short, thin, robust toxas (Figs 4,15), with only slight angular central curvature and slightly swollen (centrangulate) at centre, and with straight (unreflexed) points (length 8-13.7-23μm; width 0.5-0.9-1.5μm).

In situ observations. Field and laboratory observations were made over a period of several weeks in 1987 (M.K-B.). In the field, the capitum is easily dislodged from the apex of the fistule with only moderate movement of the water column above the specimen. Several dislodged capitate structures were observed lying on sand, in coral reef interstices and seagrass beds in the vicinity of Motupore Island. Laboratory observations on several intact specimens suggest that the capitum may have an asexual reproductive function. Several observations were made: 1, several capitate structures were carefully detached from transplanted aquarium specimens, through gentle movement of the water column directly above specimens. After detachment, capitate structures rolled over the aquarium floor until they became wedged in substrate; 2, after 24 hours of resting on the substrate the dendritic exhalant canal tubes, easily visible within the capitum (Fig. 1), extended towards and became attached to the substrate, forming a plate-like, basal, anchoring structure; 3, 36-48 hours after detachment these spherical capitate structures deflated, slightly flattened at the apex, and spread laterally into a thickened plate with single apical oscule.

Field observations in the Gulf of Thailand (J.N.A.H. and M.R.) also noted that these capitate structures are elaborate exhalant devices. Small particles of silt and other detritus were observed to be periodically expelled from the small oscules scattered over the capitum. Ostia (inhalant pores) were not seen.

Remarks

Oceanapia sagittaria is unique amongst all oceanapiids (in fact, as far as known, amongst all sponges), in having the peculiar capitate structure on the apex of its primary fistule. Bergquist (1965: 155) first hypothesised that these 'terminal caps', apparently observed free floating in the Palau Islands, might be asexual dispersal mechanisms. We confirm this idea in the present study, and suggest that this structure is the first documented case of a specialised asexual propagule recorded for the Haplosclerida, although many cases of 'unspecialised' surface and basal buds are known for several Hadromerida (e.g. *Polymastia* (Battershill & Bergquist, 1990), *Tethya* (Bergquist & Kelly-Borges, 1991), *Aaptos* (Bergquist, 1968)).

The holotype of *O. sagittaria* was apparently originally deposited in the Zoological Museum at Cambridge University, but this material has not been mentioned since Sollas's (1902) publication and it is unknown if it still survives. A spicule preparation of the holotype is also apparently located in the Natural History Museum, London (BMNH 1938.8.7.3), but this preparation contains no details of skeletal structure (F. Wiedenmayer, pers.comm.). Although *O. sagittaria* has now been described from three separate collections, only the description of Bergquist (1965), based on preserved material, is adequate by modern standards. Sollas (1902) provided an extremely brief description, essentially only describing spicule shape and size, without any useful information on skeletal structure. Oxeas were cited as 300-350×10-13μm, sigmas 12-16μm long, and toxas were 49μm long. Burton (1934) did not provide any details of the Great

Barrier Reef material, but merely compared his and Sollas's fragments. Bergquist's (1965) more detailed description of Palau Islands specimens gave spicule measurements as: oxeas (325-375× 5.5-10μm), centrangulate sigmas (10.5-20.5μm long), and toxas (36-50μm long). These dimensions, compared to those seen in the Gulf of Thailand specimens, indicate that the species is relatively homogeneous across its range, although live colouration differs slightly: Burton (1934) reported that Great Barrier Reef material was magenta and ultramarine, whereas both the present specimens and those described by Bergquist (1965) were simply red-brown or bright red, respectively.

Oceanapia sagittaria has been previously included with the family Chalinidae Gray (or its synonym Adociidae de Laubenfels), whereas it is clearly a member of the Oceanapiidae and consequently defined in this family in the present study. The Chalinidae have a more-or-less regular, unilayered, unispicular, isotropic, tangential ectosomal skeleton, with three-sided spicule meshes. In *Oceanapia* this peripheral skeleton may also be regular, isodictyal, with vaguely triangular meshes, but the tangential layer of spicules is substantially more dense and the nodal spongin, prominent in many species of Chalinidae, is usually absent (Fig. 16). Similarly, choanosomal structure in the Chalinidae is ladder-like, with uni-, pauci- or multispicular tracts, whereas in *Oceanapia* primary ascending fibres are multispicular, supporting the dense tangential ectosomal skeleton, and supplemented by a secondary (isotropic) reticulation of single spicules lying between the main fibres (Figs 10,11,18) (de Weerdt, 1985).

In the strict sense, the present species belongs to the nominal genus *Biminia*, in having both centrangulate sigmas and toxa microscleres in a fistulose, reinforced oceanapiid skeleton. However, de Weerdt (1985) and de Weerdt & van Soest (1986) argue that these microscleres may represent the retention of a primitive character and hence not valid at the generic level. They suggest that the genus should be dropped into synonymy with *Oceanapia* as the two nominal genera are virtually identical in all other respects. Several other haplosclerids have both sigma and toxa microscleres, including species of Chalinidae (e.g. *Orina*) and Callyspongiidae (e.g. *Callyspongia*). *Orina* lacks the disctinctive pulpy, reinforced, multispicular choanosomal skeleton of *Oceanapia*, having instead a unispicular, isotropic choanosome, and *Callyspongia* has a distinctive network of tangential primary, secondary, and occasionally tertiary fibres in the ectosomal skeleton, and typically regularly reticulate, wide-meshed, choanosomal fibres cored by single or few spicules. Both Burton (1934) and Wiedenmayer (1977) discuss examples of this convergence between *Oceanapia* (as *Biminia*), *Orina* and *Callyspongia* further.

An alternative point of view, offered by de Weerdt & van Soest (1986), is that the distribution of 'biminias' may reflect a possible Tethyan distribution of their common ancestor, although they are sceptical about whether this combination of characters is an apomorphy for *Oceanapia* [as inferred by Wiedenmayer (1977) and Hooper (1984)], or whether it is a synplesiomorphy and thus contains no phylogenetic information [as proposed by van Soest (1980)]. Further analysis of this possibly ancestral, possibly Tethyan distribution should be made by comparing the distributions of both the 'biminia' and non-biminid groups of *Oceanapia*, and the comparative distributions of the *Orina* and *Reniera* groups of Chalinidae. However, much of the type material relevant to this analysis, presently unavailable, firstly requires re-examination.

In addition to *O. sagittaria* there are five other species of *Oceanapia* that fit in the 'biminia' group: *Oceanapia toxophila* Dendy, 1922:45 from Providence I., Seychelles Is, western Indian Ocean (holotype BMNH 1921.11.7.37 re-examined); *O. stalagmitis* (Wiedenmayer, 1977:124) from the Bahamas; *O. ooita* (Hoshino, 1981:122) from Japan; *O. macrotoxa* (Hooper, 1984:55) from the Timor and Arafura Seas, northwest Australia (holotype NMV F51373); and *O. cancap* de Weerdt & van Soest, 1986:39 from the Madiera region, West Africa, southeast North Atlantic. In addition to these taxa, re-examination of Ridley's (1884:424) material of '*Gellius fibulatus*' from Torres Strait, Qld (BMNH 1822.2.23.281) found that it is neither a chalinid nor conspecific with *Reniera fibulata* Schmidt, 1862, but belongs to Oceanapiidae and furthermore appears to be identical to *O. macrotoxa*. The identity of an Indonesian specimen collected by the *Siboga* expedition (ZMA POR 1709), cited as *O. toxophila* by de Weerdt (1985:81), is not certain, but it too is possibly conspecific with *O. macrotoxa*. An alternative point of view is that these three nominal Indo-west Pacific 'biminia' species, *O. toxophila*, *O. macrotoxa* and *O. ooita*, may be geographic variants of a single, widely distributed species, extending from the Seychelles Islands to Japan, Indonesia, northwest and northeast Australia.

Apart from the peculiar capitum seen in *O. sagittaria*, there are few major differences between any of the 'biminia' species in external morphology, skeletal structure, spicule geometry or spicule size (as noted by Hooper, 1984: table 1). Thus, it would be equally justifiable to synonymise all six known 'biminia' species as it would be to combine the three Indo-west Pacific species on the basis of these conventional morphometric characters. For the present we maintain all these species in the 'biminia' group, but recognise that only more comprehensive collections of *Oceanapia* throughout the Indo-Pacific may discover material with intermediate characteristics, resolving present doubts.

Apart from the peculiar capitum, *O. sagittaria* is most similar to *O. toxophila*. However, oxeas are sharply pointed, fusiform, or occasionally mucronate in the present species, whereas in *O. toxophila* they are hastate or rounded; oxea size is relatively homogeneous within both species but substantially larger in *O. sagittaria*; microsclere dimensions are similar in both species (see dimensions below for *O. toxophila*), although *O. toxophila* has both c-shaped and contort sigmas, and *O. sagittaria* was discovered to have a morphologically distinct, smaller category of centrangulate, robust toxas, not previously described for the species. Although these differences in spicule size and geometry could be construed as being relatively trivial, they are certainly as substantial as any of the differences between all other 'biminia' species.

Morphological characteristics of other 'biminia' species are as follows. *Oceanapia toxophila* Dendy has a tubular, burrowing, globular, simple base, with very thin, single fistules on each end of the body (the larger, open fistule is apical, the smaller, blind fistule is a basal rootlet); fistules up to 50mm long, 5mm diameter; ectosomal skeleton is a detachable, thin, unispicular, subisodictyal crust; choanosomal skeleton contains both reticulate, multispicular bands and a dense feltwork of subisodictyal spicules; oxeas hastate or rounded, mostly blunt (265-315×5-12μm); microscleres are only moderately common; sigmas very small, c-shaped or contort (12-26×0.5-1.5μm); toxas sharply angular at centre, straight arms, slightly reflexed points (12-55×0.5-2.5μm) (redesribed from the holotype BMNH 1921.11.7.37 (RN XX.2) and Dendy (1922) in part).

Oceanapia stalagmitis (Wiedenmayer) has a semi-incrusting, burrowing, massive base, with multiple, short, open and blind fistules on upper surface, rhizome-like blind fistules on under surface; fistules up to 17mm long, 10mm diameter; ectosomal skeleton a dense, subisodictyal, unispicular layer over a denser detachable crust; choanosomal skeleton an irregular reticulation of both stout and thin fibres, with unispicular subisodictyal spicules dispersed between; oxeas usually sharply pointed, fusiform (100-155×3.5-5μm); microscleres abundant; sigmas centrangulate, c-shaped (11-32×0.5-1μm); toxas small, slight central curvature, straight arms, very slightly reflexed points (10-32×0.5-1μm) (Wiedenmayer, 1977).

Oceanapia ooita (Hoshino) has a massive, subspherical, burrowing base, with numerous, open, wide fistules on upper surface, and rhizome-like, blind fistules on under surface; fistules up to 40mm long, 8mm diameter; ectosomal skeleton dense, unispicular, subisodictyal; choanosomal skeleton with densely packed, longitudinal spicule tracts, interdispersed with subisodictyal single spicules; oxeas homogenous, abruptly pointed, hastate (180-218×7-9μm); microscleres abundant; sigmas c-shaped, centrangulate (14-35xup to 1μm); toxas slightly curved at centre, straight arms, straight points (up to 45μm, thin) (Hoshino, 1981).

Oceanapia macrotoxa (Hooper) has a burrowing, massive, subspherical base with many long, thin, open and blind fistules on the upper surface, and smaller, thinner, rhizome-like blind fistules (rootlets) on the under surface; fistules are up to 60mm long, 8mm diameter; ectosomal skeleton is a thick, detachable, unispicular, subisodictyal crust; choanosomal skeleton with multispicular tracts, some ascending as well as uni- or paucispicular, subisodictyal tracts dispersed between; oxeas are divided into two indistinct size classes, fusiform to subhastate, mostly sharply pointed (94-260×1.5-7μm, 171-279×6-11μm); microscleres abundant; sigmas are small, centrangulate, c-shaped (9-35×0.5-2.0μm); toxas have angular central curves, straight arms and reflexed points (8-82×0.4-3.5μm) (Hooper, 1984).

Oceanapia cancap de Weerdt and van Soest is burrowing, fistulose, although the base is unknown; fistules are open, single or bifurcate, up to 80mm long, (?) 50mm diameter; ectosomal skeleton unispicular, tangential, subisodictyal; choanosomal skeleton (only known for fistule walls) is longitudinal, branching and anastomosing, multispicular tracts with interdispersed subisodictyal single spicules; oxeas fusiform, sharply pointed (up to 320×8μm); sigmas c-

shaped, centrangulate (20μm, thin); toxas with slight central curvature, straight arms, slightly reflexed points (50-75μm, thin) (de Weerdt and van Soest, 1986).

ACKNOWLEDGEMENTS

We are most grateful to Wallie de Weerdt and Jane Fromont, both of who provided invaluable comments and greatly improved our interpretation of this species. We also thank Peter Murphy (AIMS, Townsville) for providing the opportunity for J.N.A.H. and M.R. to travel to and collect from the Thai region; Motupore Island Research Station, University of Papua New Guinea, for providing facilities for M.K-B.; Shirley Stone (BMNH, London) for assisting the senior author in locating particular sponges amongst the vast BMNH collections; and Leonie Hooper for patiently inking all the line drawings.

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A NEW SPECIES OF *NYCTIMYSTES* (ANURA: HYLIDAE) FROM THE STAR MOUNTAINS, PAPUA NEW GUINEA

STEPHEN J. RICHARDS AND GREGORY R. JOHNSTON

Richards, S.J. & Johnston, G.R. 1993 06 30: A new species of *Nyctimystes* (Anura: Hylidae) from the Star Mountains, Papua New Guinea. *Memoirs of the Queensland Museum* **33**(1): 73-76. Brisbane. ISSN 0079-8835.

Nyctimystes oktediensis sp.nov. is a member of the *N. papua* group. Morphologically, it is similar to *N. disrupta* from which it can be distinguished by its brown iris, reduced finger webbing, and palpebral venation of vertical to oblique lines over most of the eyelid. *N. oktediensis* is a stream-dwelling species inhabiting lower montane rainforests in the rugged Ok Tedi headwaters region of western Papua New Guinea. □ *Hylidae, Nyctimystes oktediensis, new species, Papua New Guinea.*

Stephen Richards, Zoology Department, James Cook University, Townsville, Queensland 4811, Australia; Greg Johnston, School of Biological Sciences, Flinders University, Bedford Park, South Australia 5042, Australia; 5 November, 1992.

The montane hylid genus *Nyctimystes* is characterised by the presence of vertical pupils and palpebral venation (Zweifel, 1958). Twenty-three species are presently known, with 21 from the island of New Guinea (Zweifel, 1958; 1983), one species in northern Queensland, Australia (Czechura, Ingram & Liem, 1987) and another in the Moluccas.

Within *Nyctimystes* a distinctive, and presumably monophyletic, group of species has been referred to as the *N. papua* species group (Zweifel, 1983). Members of this group are moderate to large in size, have sparse or much reduced palpebral venation, lack a vocal sac in males, have short, high, rounded snouts, and the outer fingers are no more than one half webbed. Although Zweifel (1983) recognised only four species in the group, he was aware of several specimens that could not be allocated to any known species.

In November 1991, we surveyed the frog fauna of the upper Ok Tedi drainage basin on the southern slopes of the Star Mountains, central New Guinea. We collected 36 species, of which almost one half could not be allocated to any known taxon. The only *Nyctimystes* that we encountered was an undescribed member of the *N. papua* group. Our specimens were most similar morphologically to *N. disrupta* but had a brown iris, reduced webbing between the fingers, and less disrupted palpebral venation.

Measurements and terminology follow Zweifel (1983). Abbreviations used in the text are: SV, body length from snout to vent; TL, tibia length; FT, foot length; HD, hand length; EN, eye to naris distance; IN, internarial distance; SN, snout to naris distance; HW, head width; EY, eye diameter.

Specimens are housed in the Queensland Museum (QM), South Australian Museum (SAM), Biology Department, University of Papua New Guinea (UP) and the American Museum of Natural History (AMNH).

Nyctimystes oktediensis sp.nov.
(Figs 1-3)

MATERIAL EXAMINED

HOLOTYPE: QM J56896 adult male with nuptial pads, collected by S.J. Richards & G.R. Johnston at 1625m, 23 November 1991 on the southeastern slopes of Mt Akrik, Star Mountains, Western Province, Papua New Guinea (5°10'S, 141°10'E).

PARATYPES: QM J56897-8, SAM R40771 three adult males with nuptial pads, same data as holotype but collected on November 24, 1991; UP 5137-9, three adult males with nuptial pads collected by D. Hyndman, 16 February 1975, from a stream adjacent to the Bleil Bil hunting lodge at Kamfon (2200m), Kam Valley, Star Mountains, Western Province, Papua New Guinea.

DIAGNOSIS

Nyctimystes oktediensis is distinguished from its congeners by a combination of the following characters: palpebral pigmentation relatively sparse; males without vocal sac; iris brown in life; fingers less than half webbed; tympanum indistinct but visible; moderately large size (males 60.8-67.2mm SV).

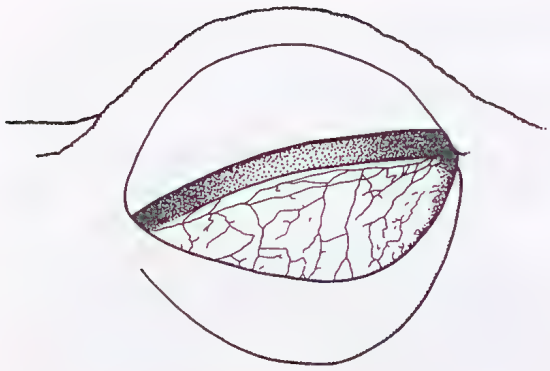

FIG. 1. Right eye of *Nyctimystes oktediensis* (holotype) showing palpebral venation.

DESCRIPTION OF HOLOTYPE

Adult male with the following measurements and proportions: SV 60.8; TL 35.8; HW 21.8; EY 7.8; EN 5.0; IN 6.5; SN 3.5; HD 24.0; FT 32.1; width of third finger disc 4.4, width of third penultimate phalanx 2.7; width of fourth toe disc 3.8, width of fourth penultimate phalanx 3.0; TL/SV 0.588; HW/SV O.358; EN/SV 0.082; EY/SV 0.128; IN/SV 0.106; EN/IN 0.769.

Snout short, high, rounded in dorsal view, almost vertical in lateral view; canthus rostralis distinct, slightly curved; loreal region steep, slightly concave; nostrils directed laterally (quite evident in dorsal aspect), internarial distance distinctly greater than distance from eye to naris (EN/IN 0.769). Pupil vertical. Palpebral pigmentation of vertical to oblique lines over entire eyelid, with few broken, interconnecting horizontal lines, slightly weaker posteriorly (Fig. 1). Tympanum indistinct but visible, dorsal one quarter of tympanic annulus hidden by postocular fold. Vocal sac absent. Vomerine teeth in two transverse rows between the internal nares.

Relative lengths of fingers 3>4>2>1; scanty webbing between third and fourth fingers, reaching halfway to distal subarticular tubercle on fourth, and to proximal tubercle on third; subarticular tubercles single; disc of third finger more than half eye diameter. A finely granular nuptial rugosity on inside of first finger. Relative lengths of toes 4>5=3>2>1, webbing almost to discs on all toes except fourth, fourth toe webbed to just short of distal subarticular tubercle; subarticular tubercles rounded, single; a low, oval inner metatarsal tubercle but no outer one (Fig. 2).

Dorsal surfaces slightly rugose, without conical asperities. A strong fold from posterior corner of eye to above arm insertion. Ventral surfaces granular. No heel lappet. Dorsally olive green. Lateral surfaces mottled olive gold and dark brown. Limbs and back (posteriorly) with a mozaic of olive green patches edged with dark brown, and interspersed with olive gold tending to form bands across the limbs. Venter speckled with cream and grey, iris brown (Fig. 3).

VARIATION

The smallest specimen, the holotype, has more widely spaced nares than the paratypes (EN/IN 0.769 vs 0.800-1.00). While the palpebral venation is similar in all of the type series, there is some variation in the degree to which the oblique lines are interconnected horizontally, and the venation of one specimen (QM J56898) is scarcely detectable on the posterior one quarter of the right eyelid (clearly visible on left eyelid). Proportions of the paratypes are as follows: TL/SV 0.583-0.627; HW/SV 0.342-0.356; EN/SV 0.080-0.087; EY/SV 0.110-0.127; IN/SV 0.082-0.100; EN/IN 0.800-1.00.

COMPARISON WITH OTHER SPECIES

The reduced palpebral venation, lack of a vocal sac, snout shape, basal finger webbing and size of *N. oktediensis* show that it is a member of the *papua* group defined by Zweifel (1983). However, *N. papua* is a much smaller species, with females smaller or about the same size as male *N. oktediensis*, and has only a few flecks of black pigment in the anterior corner of the lower eyelid (Menzies, 1975; Zweifel, 1983). Even allowing for greater variation when additional specimens are collected (see Zweifel, 1983), palpebral venation of this species is unlikely to approach the state of *N. oktediensis*. *N. trachydermis* is larger than *N. oktediensis* (smallest male *N. trachyder-*

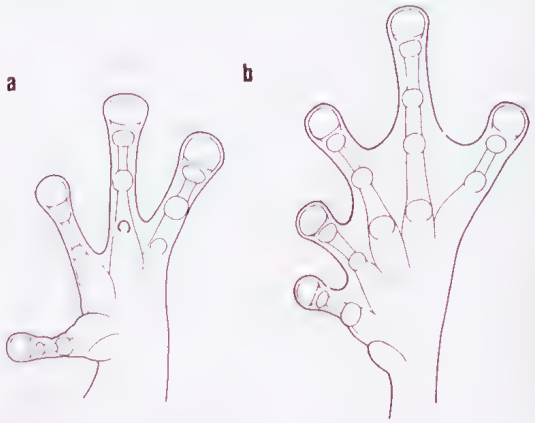

FIG. 2. Left hand (a) and foot (b) of *Nyctimystes oktediensis* (holotype) in palmar and plantar view respectively.

FIG. 3. Holotype of *Nyctimystes oktediensis* in life.

mis 71.6mm), has conical asperities on the dorsum, and a completely concealed tympanum. The sole specimen of *N. tyleri* (a male) is also much larger (78mm), and had a bright yellow iris (brown in *N. oktediensis*) in life (Zweifel, 1983). *N. disrupta* is similar in size to *N. oktediensis* but has a green iris in life, more extensive webbing between the fingers, and palpebral venation of very fine, disrupted lines (Zweifel, 1983).

Habits and Habitat

The Mt Akrik specimens were collected at night from branches overhanging the Ok Kun, a steep rainforest stream draining into the Ok Tedi. None was heard calling, and additional observations are required to determine whether this species can vocalise. At least four species of suctorial tadpoles were collected at this site, but we are unable to associate any of these positively with *N. oktediensis*.

Distribution

Currently known only from the Star Mountains in central New Guinea.

Etymology

Named for the rugged upper Ok Tedi drainage basin where all of the types were collected.

REMARKS

Zweifel (1983) discussed several samples of *N. disrupta*- like specimens that he was unwilling to assign to any known taxon. All of these have finger webbing typical of *N. oktediensis* but most show characters distinguishing them from this species. Two specimens from Irian Jaya (AMNH 49671, 49674) are quite distorted, making accurate measurements impossible, and we are unwilling to assign these to *N. oktediensis* without fresh material. An adult male from Telefomin (AMNH 114817) agrees well with the type series, although the colour of the iris in life is unknown, and we tentatively assign this specimen to *N. oktediensis*. Specimens from Okefomin (AMNH 11485-6), Ialibu (AMNH 81025-6), and Wagau (AMNH 74816-7) have much less palpebral venation than *N. oktediensis*. A series of adult males from Nipa, Southern Highlands (AMNH 103184-8) are large (to 72mm), extremely rugose dorsally (but without conical asperities), and have a completely hidden tympanum. They clearly represent a species distinct from *N. oktediensis* and all other described *Nyctimystes*.

Hyndman & Menzies (1990) list two unassigned species of the *Nyctimystes papua* group from the Ok Tedi region. Their *N.*(?) *papua* (UP 6719) possesses a vocal sac and thus is not a member of this group. The specimens listed as *N.* cf *disrupta* (UP5137-9) agree with *N. oktediensis* in all respects, and are included in the type series.

ACKNOWLEDGEMENTS

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THE TAXONOMY AND DISTRIBUTION OF *PETAURUS GRACILIS* (MARSUPIALIA: PETAURIDAE), WITH NOTES ON ITS ECOLOGY AND CONSERVATION STATUS

STEVE VAN DYCK

Van Dyck, S. 1993 06 30: The taxonomy and distribution of *Petaurus gracilis* (Marsupialia: Petauridae), with notes on its ecology and conservation status. *Memoirs of the Queensland Museum* 33(1): 77-122. Brisbane. ISSN 0079-8835.

Petaurus gracilis is morphologically and biochemically distinct from *P. norfolcensis* from which it is geographically isolated. Since its description in 1883, *P. gracilis* has been recorded from 22 localities between Ingham and Tully (80km) in coastal lowland woodland below the 90m contour. Its restricted distribution is determined by very high seasonal rainfall, a mean dry quarter precipitation usually greater than 100mm and a woodland blend of vegetation that is shaped and maintained by fire. The presence of one of the northern bloodwoods (*Eucalyptus intermedia*, *E. clarksoniana* or *E. dolichocarpa*) and an accompanying species of 'bird-syndrome' arillate *Acacia* are suggested as a minimal basis for suitable habitat. Among exudivores, *Petaurus gracilis* appears to be more a dietary opportunist, feeding on nectar, pollen, arthropods, *Acacia* exudates, lerp, and honeydew when these items become seasonally available. More notable dietary items include *Acacia* arils, *Xanthorrhoea* scape exudates and sap (or kino) of *E. intermedia*. Interpretation of its socioecology was impeded by small sample size but home range size for an adult female was determined at 23ha and a quasi-polygynous mating system was suggested. *Petaurus gracilis* is endangered throughout its range by habitat destruction, fragmentation and changes in local fire regimes that together have resulted in an 80% loss of its preferred habitat. □ *Petaurus gracilis, Petaurus norfolcensis, Petauridae, taxonomy, distribution, conservation, Queensland, Australia, Mahogany Glider, habitat, ecology, tropical woodland, diet, behaviour.*

Steve Van Dyck, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 21 February, 1993

Since its description in 1883 by Charles de Vis, the taxonomic status and distribution of *Petaurus gracilis* has been a matter for conjecture. De Vis failed to designate a holotype and no specimens are referred to in the literature or known from collections outside the Queensland Museum. Five years after its description, Thomas (1888) synonymized *P. gracilis* with *P. norfolcensis* (then *Petaurus sciureus*) and Mackay (1988) dealt with it similarly. Other references to the name *P. gracilis* deal with it as a northern subspecies of *P. norfolcensis* (Iredale & Troughton, 1934; Troughton, 1941; Tate, 1945; Fleay, 1947; 1954; Marlow, 1962; Suckling ,1983; Alexander, 1981; Colgan & Flannery, 1992). Given the lack of *P. gracilis* specimens in collections, and the subsequent anonymity of the species, it is probable that its synonymy has resulted from a broad interpretation of de Vis's brief description rather than from a physical examination of the few *P. gracilis* specimens. Also, the assigning of *P. norfolcensis gracilis* to a wide range of Queensland examples of *P. norfolcensis* has resulted from too broad an interpretation of de Vis's loose reference to its collection locality, 'North of Cardwell' (de Vis, 1883: 620).

In 1990 I reported three previously unregistered museum specimens, whose large size, long, thin, short-haired tails, pattern of fur colouration and measurements agreed closely with de Vis's description of *P. gracilis* (Van Dyck, 1990). These skins had been collected by Kendall Broadbent in 1886, from somewhere on, or near Mt Echo, 18km SW Cardwell. At the time of that report, given the faded, deteriorated quality of the skins, the fragmentary nature of cranial and dental material extracted from them, and inexplicable inconsistencies between the de Vis description and data associated with old identification tags attached to the skins, it was concluded that until additional material came to hand, *P. gracilis* should remain a junior synonym of *P. norfolcensis*. However, I also concluded that it was inappropriate to continue the use of *P. norfolcensis gracilis* in respect of all northeastern and mideastern Queensland examples of *P. norfolcensis* as they were indistinguishable from their more southern conspecifics.

In December 1989, living representatives of *P.*

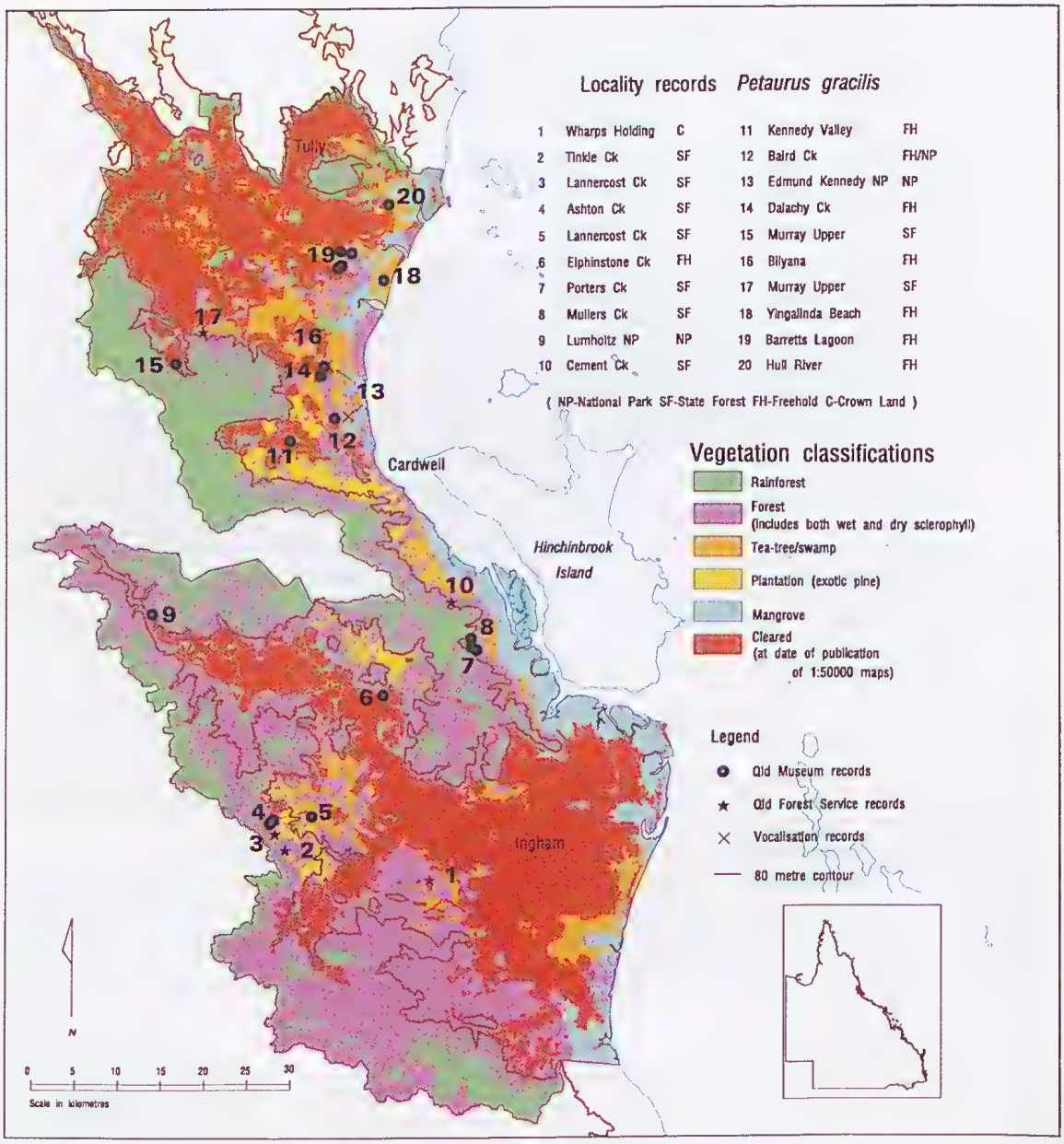


FIG. 1. Locality records for *Petaurus gracilis* (see Table 1 for details).

gracilis were located on freehold land at Barretts Lagoon (18°02'S, 145° 58'E), 14km SE of Tully. At that time, one specimen (JM7605) was collected for museum accession. In January 1990 the collection site was cleared for cultivation of bananas and pineapples. In February 1991 an adult female was captured nearby, photographed (Fig. 2) and subsequently (May) released at the site of capture (Van Dyck, 1992a). Further surveys conducted during 1991-2 extended and refined the range of the species and provided data suggesting that the long-term conservation of the species could be a matter of grave concern.

The aim of the present study was to: 1, clarify the taxonomic status of *P. gracilis* with respect to *P. norfolcensis* (in particular) and other members

of the genus; 2, provide preliminary data on the distribution, habitat requirements, diet and socioecology of *P. gracilis*; and 3, assess the conservation status of the species.

METHODS

Systematics

Nomenclature for molar tooth structure follows Woodburn et al. (1987), and cheek tooth number follows Archer (1978) (see explanation in Marshall, 1987). Dental and cranial measurements were made after the method shown in Fig. 3. Specimens were measured to the nearest 0.01mm using NSK electronic digital calipers. Specimens compared in diagnoses were adults with fully erupted fifth molars. T-tests were used to test for statistical significance.

Specimens from the following institutions were examined: Queensland Museum (specimens refered to in text prefixed by J or JM); Australian Museum, Sydney (specimens prefixed by M); Australian National Wildlife Collection, Division of Wildlife Research, Canberra; Bishop Museum, Honolulu; British Museum (Natural History), London; American Museum of Natural History, New York; Museum of Victoria, Melbourne. Maximum numbers of individuals included in statistical analyses were: *P. norfolcensis* 70, *P. breviceps* 21, *P. australis* 11, *P. abidi* 5 and *P. gracilis* 11. Old skins (JM5521, JM5522, JM5523) were omitted from statistical analyses.

Field Surveys

Field observations and surveys were made during the following periods: 1-13 Dec 1989, 9-24 Feb 1991, 9-24 May 1991, 2-16 Aug 1991, 23-29 Nov 1991, 29 Feb-13 Mar 1992, 13-14 May 1992, 24 May-6 June 1992, 26 Sept-11 Oct 1992, 24-26 Nov 1992. Fieldwork during 1989 and 1991 concentrated on capture and radiotelemetry of individuals at Barretts Lagoon, while 1992 fieldwork was concerned with an assessment of distribution outside the immediate area of the lagoon.

Capture Techniques

Wire cage and aluminium live traps were set 2-7m above the ground. Traps included Elliott aluminium (460×160×150mm and 330×95×100mm) Mascot wire (560×205×215mm),

FIG. 2. Adult female *Petaurus gracilis* T4026, caught Barretts Lagoon 22 Feb 1991, released 11 May 1991.

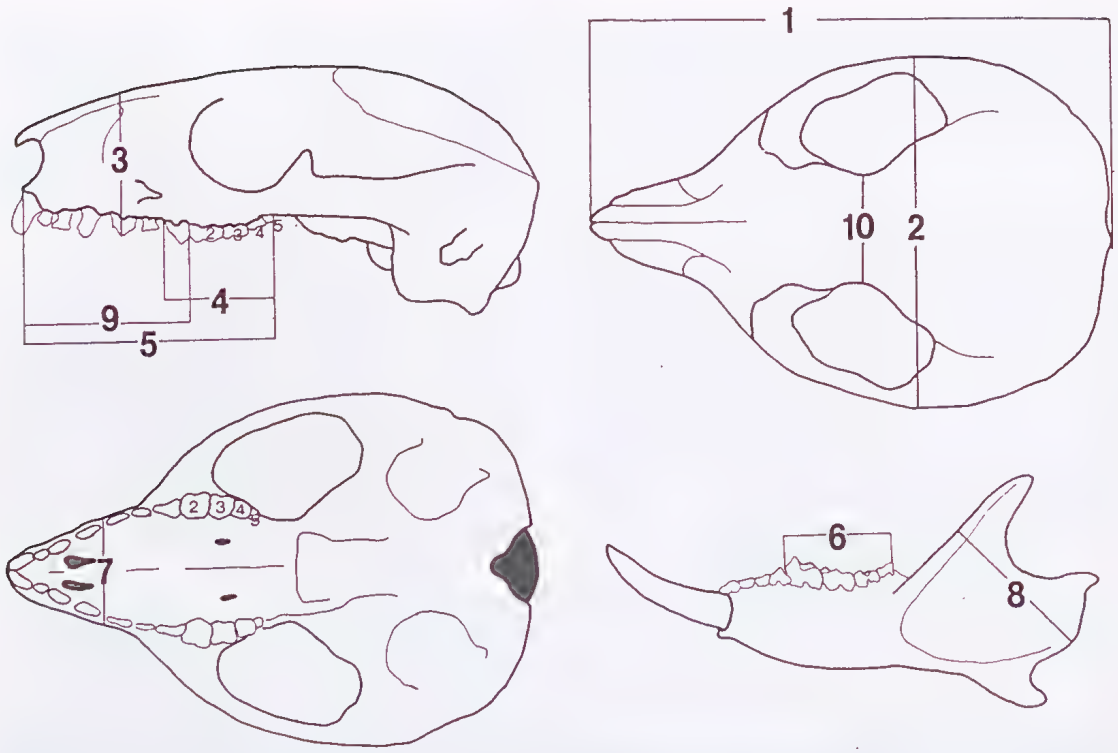


FIG. 3. Method used in skull and tooth measurement: 1, maximum skull length; 2, zygomatic width; 3, rostrum height; 4, upper molar row length; 5, upper tooth row length; 6, lower molar row length; 7, rostral width between upper canines; 8, width of ascending ramus; 9, upper incisor-premolar row; 10, interorbital width.

Tamohawk wire (400×140×140mm) and Acme wire (440×200×180mm). Traps were protected by plastic bag weather shields and supported on horizontal ply baseboards screwed to right-angle iron brackets which were nailed to tree trunks. Baits consisted of a sugar/honey toffee or a mixture of honey and sweetened condensed milk. Additional attractants of diluted honey, sugar water or raspberry cordial were sprayed on tree trunks near trap entrances to lure gliders into the traps. Traps were laid along transects on trunks of living and dead trees, or arranged in groups of up to 12 among flowering *Xanthorrhoea johnsonii* chosen for signs of *P. gracilis* visitation by way of footprinted flower stalks. Trapping was carried out during the following periods: 1-13 Dec 1989 (205 trap nights); 9-24 Feb 1991 (230 trap nights); 9-24 May 1991 (110 trap nights); 29 Feb-13 Mar 1992 (176 trap nights). Trap-nights totalled 721 and covered 10 sites at Barretts Lagoon and one at Edmund Kennedy National Park, Cardwell.

At the beginning of the survey (Feb and May 1991), 48 artificial nesting hollows were installed and left for between 16-19 months at 2 sites at Barretts Lagoon to act as a back-up should the trapping program fail. Of these, 34 were attached to tree trunks (Feb 21) at the Barretts Lagoon 'Rice Fields' (18°01'S, 145°58'E) where an adult female had been caught (19 Feb). This 200-400m wide strip of woodland was bordered to the west by Barretts Lagoon Road and to the east by natural treeless swales (Fig. 19). Given the irregular shape of the site, the 34 hollows were arranged in a grid of six rows (1 row of 7 hollows, 2 of 6, 3 of 5) with minimum spacings of approximately 50m. On 17 May 1991, 14 additional artificial nests were installed further east (18°01'S, 145°59'E) and set along 700m of north-south track and spaced at 50m. The choice of 'nest' design was based roughly on the trap of Mawbey, (1989) which was shown to be highly effective for catching sugar gliders *P. breviceps* in the field. The artificial nesting hollows used in my study were of 160mm (diameter) PVC sewer pipe cut to 500mm lengths, capped at either end and

FIG. 4. One of 48 PVC artificial nest hollows used in the survey. Each was strapped onto a trunk with fencing wire.

drilled with a 65mm (diameter) entrance hole 120mm from the top of the tube (tube vertical). These hollows were furnished internally with a 280mm 'ladder' of roughened timber screwed directly below the entrance hole while the floor was perforated for drainage. All tubes were painted a dull brown-green, numbered and strapped vertically to trunks at heights of 3-7m using fencing wire (Fig. 4). All tubes were inspected at least once per survey period and all but one (occupied by a family of *P. breviceps*) were removed from the two sites by 8 Sept 1992.

One *P. gracilis* (Fig.2) was captured in a mist-net enclosure constructed around the outside of its den in a hollow Swamp Mahogany trunk (see Van Dyck, 1992a). Two were captured by 'port-holing' hollow trunks of known nest trees. This practice involved cutting a rectangular hole (approx 120mm × 180mm) into the den and extracting the glider(s) by hand. The 'port-hole' was then plugged with a hardwood block which was wired for later access. One individual was caught by shaking it from a small tree (see Van Dyck, 1992b).

Handling and Radio-tracking Procedures

Captured individuals were weighed, measured, sexed, assigned to an age category from the condition of wear of the first upper incisors (Suckling, 1980; Alexander, 1981), tagged on one ear with a numbered (T40_ _) fingerling ear-tag ('FF', Salt Lake Stamp Co., Utah) and (where possible) released back into the den from which they were taken. Gliders used in radio tracking were fitted with a Titley (Ballina, NSW) 'Microlite', two-stage transmitter either attached to a soft leather collar with a protruding 15cm whip antenna or epoxy-potted into a small disc (diameter 26mm × 10mm high) with a protruding 28cm antenna. The ventral surface of the epoxy disc transmitter was glued to the animals mid-back (Selleys Supa Glue) after a circle of fur approximating the diameter of the disc had been cropped close to the glider's skin. The short hair stubble that remained, provided a rough bonding surface for the glue on the transmitter and at the same time protected the animal's skin from contact with the adhesive. Long hair surrounding the positioned disc was then glued over the dorsal surface of the transmitter, in effect hiding it and leaving only the whip antenna exposed. The total weight of the transmitter package was approximately 11g. A 2000 channel 'Regal 2000' (Titley) portable receiver operating on the 150.000-151.999mHz band, and a 2 element hand-held H-frame antenna were used to locate animals.

Home Range Determination

Preliminary home range estimates were determined for one adult female (T4026) and two sub-adult female gliders (T4027 and T4028, presumed to be the offspring of T4026). During the course of the study only one male (T4030) was captured and radio-tagged. This male dislodged its transmitter on the third day and only den site data was recorded. Although gliders were strictly nocturnal, a morning (0600hrs) and afternoon (1600hrs) den fix was usually taken for each tagged animal. Because animals proved difficult to catch and visits to the area were irregular (and often 3-4 months apart), animals were radio-tracked both continuously and randomly during each visit. Direct observation was used to maximise return of information other than that associated solely with home range. Trees visited on a

Site	Locality	Lat.	Long.	Alt.m asl.	Nature of record (No. recorded)	Dates	Collector/ Observor	Tenure
i	"North of Cardwell"	—	—	—	species description de Vis (1883)	1883	K. Broadbent	—
ii	"Mt Echo"	—	—	—	JM5521 (AM) JM5522 (AF) JM5523 (AF)	1886	K. Broadbent	—
1	*Wharps Holding	18°41'18"S	146° 04'25"E	20-40	sighting (2)	13.10.92	L. Logan T. Eyre	Crown
2	*Tinkle Creek	18°39'20"S	145°54'55"E	40	sighting (1)	15.10.92	T. Eyre	S.F.
3	*Lannercost Creek	18°38'20"S	145°54'15"E	90	sighting (1)	15.10.92	T. Eyre	S.F.
4	Ashton Creek	18°37'41"S	145°53'57"E	70	sighting (1)	01.06.92	S. Van Dyck S. Burnett	S.F.
		18°37'26"S	145°54'12"E	60-70	sighting (2)	01.06.92	"	S.F.
5	Lannercost Creek	18°37'13"S	145°56'44"E	30-40	sighting (1)	01.06.92	"	S.F.
6	Elphinstone Creek	18°29'42"S	146°01'26"E	20-40	sighting (1)	11.03.92	"	Freehold
7	Porters Creek	18°26'57"S	146°07'35"E	35	JM9015 (AF)	10.03.92	"	S.F.
		18°26'47"S	146°07'17"E	35	sighting (1)	13.05.92	S. Van Dyck J. Kehl I. Rob	S.F.
8	Mullers Creek	18°26'13"S	146°07'15"E	20-40	sighting (2)	13.05.92	"	S.F.
9	Lumholtz N.P	18°24'30"S	145°46'10"E	40-60	sighting (1)	11.03.92	S. Van Dyck S. Burnett	N.P.
10	*Cement Creek	18°23'55"S	146°05'57"E	20-40	sighting (1)	12.10.92	C. Corben	S. F.
11	Kennedy Valley	18°13'31"S	145°55'23"E	0-20	JM8549 (AF)	-.10.90	E. Gallipo	Freehold
				0-20	JM8550 (joey F)	-.10.90	"	Freehold
12	Baird Creek	18°12'11"S	145°58'17"E	0-10	sighting (1)	05.03.92	S.Van Dyck S. Burnett	Freehold/ N.P.border
13	Edmund Kennedy N.P.	18°12'04"S	145°59'14"E	0-20	call (1)	05.03.92	"	N.P.
		+18°08'43"S	145°57'50"E	0-20	call (1)	04.03.92	"	N.P.
14	Dalachy Creek	18°09'26"S	145°57'26"E	0-10	JM9014 (AM)	08.03.92	"	Freehold
		18°08'51"S	145°57'40"E	0-10	sighting (2)	03.03.92	"	Freehold
15	Murray Upper	18°08'38"S	145°47'54"E	40-60	JM9016 (AF)	10.03.92	"	S.F.
16	Bilyana	18°07'S	145°56'E	0-20	private mount	- .- .74	T. Marsilio	Freehold
17	*Murray Upper	18°06'30"S	145°49'40"E	20-40	sighting (1)	16.10.92	C. Corben	S.F.
18	Yingalinda Beach	18°03'18"S	146°01'37"E	0-10	sighting (1)	18.08.91	S. Van Dyck P. Stumkat	Freehold
19	Barretts Lagoon i. South-west bank	18°02'31"S	145°58'36"E	0-10	JM7400 (AM)	09.12.89	"	Freehold
				0-10	sighting (8)	06.12.89-08.12.89	"	Freehold
	Barretts Lagoon ii. North-east bank	18°02'23"S	145°58'46"E	0-10	sight(1) & call (1)	09.08.91	P. Stumkat	Freehold
		18°02'22"S	148°58'52"E	0-10	JM7290 (AF with joeys JM9729 & JM9730)	14.02.73	G. Gordon R.J. Grimes	Freehold
	Barretts Lagoon iii. " Rice Fields	18°01'26"S	148°58'46"E	0-10	sighting (10)	15.02.91-.02.03.92	S. Van Dyck P. Stumkat S. Burnett B.&C. Cowell	Freehold
	Barretts Lagoon iv East	18°01'33"S	145°59'34"E	0-10	sight (9) & call (2)	17.05.91-29.11.91	"	Freehold
20	Hull River	17° 58'29"S	146°02'02"E	0-20	sighting (1)	2.10.92	S. Van Dyck S. Burnett	Freehold

glider's traversed route were marked with flagging tape and surveyed during the day.

It is acknowledged that direct observation through continuous tracking may have led to an underestimation of home range size through loss of independence of fixes (Swihart & Slade, 1985). To overcome this problem, where continuous tracking was employed, 30 minute fixes were extracted from examination of each route plotted through time. Quin et al. (1992) considered that 30min radio fixes for fast moving mammals such as species of *Petaurus* were adequate to assume independence of data points. Fixes were taken from adult female T4026 over a period of 4 full nights and 13 partial nights (including den fixes) during May, August and November 1991 (110 fixes), while those from sub-adult female T4028 were taken over a period of 1 full night and 9 partial nights (including den fixes) during May 1991 (36). Fixes from sub-adult female T4027 were taken over a period of 1 full night and 6 partial nights (including den fixes) during May 1991 (36 fixes). Estimates of home range area were generated using the harmonic mean distance minimum (HM) using 95% isopleths (see Dixon & Chapman, 1980) and the minimum convex polygon (MCP: Mohr 1974). The utility and appropriateness of the HM for describing home ranges of animals such as sugar gliders was demonstrated by Quin et al. (1992). Estimates were generated with the RANGES IVm software package (R. E. Kenward; Institute of Terrestrial Ecology, Furzebrook Research Station, Wareham, United Kingdom).

Spotlighting

12 volt, 150mm and 230mm 'Powa Beam Spotlights' (Byron Bay, NSW) were used from a vehicle, the 230mm (9") 'Powa-lite' (1 million CP, quartz halogen) being particularly efficient. 150mm, 12V spotlights powered by wet cell motorbike batteries were used for on-foot surveys. 3 and 4 'D'cell 'Mag-Lite' torches (Mag Instruments - Ontario, Calif) were used to observe radio-tagged animals. The expanding beam of these torches greatly facilitated detection of gliders leaping from treetops. A total of 1334 manhours were spent spotlighting for *P.gracilis* (Table 3). *Petaurus gracilis* was consistently difficult to locate (see Davey, 1984; Menkhorst et al., 1988 for similar problems with *P. norfolcensis*). It was practically silent, evasive in spotlights and its eyes reflected poorly (dull red). Animals attracted by playback recordings of *P. norfolcensis* or *P. gracilis* vocalisations (see Kavanagh & Rohan-Jones, 1982) or by imitated calls aborted their approach if a light was turned on. In approximately 877 manhours of non-telemetry spotlighting (547 hours from a vehicle, 330 on foot), 22 of the 28 animals located by this method were first observed from a vehicle.

Palynological Analysis

Pollen analysis was undertaken by M. Dettmann (University of Qld) on five faecal samples collected between Feb and Nov 1991 from Barretts Lagoon. Two strew slides were prepared from each sample. One, contained crushed but otherwise untreated faecal material mounted in glycerine jelly under a glass coverslip. The second slide contained faecal material treated with warm 5% KOH for 5min, then washed thoroughly under distilled water and sieved through a 240μ mesh screen prior to mounting in glycerine jelly. The untreated slides were examined to estimate relative proportions of pollen, other plant tissue and insect fragments in each sample, and to estimate the proportion of pollen with their contents (intine) in place. Qualitative and quantitative analyses of the pollen assemblages represented in each sample were determined from the treated slide.

Vegetation Analyses

At each site where a glider had been observed (Table 1) the vegetation was assessed visually and classified into one of the vegetation types of Tracey (1982). A vegetation proforma was prepared by W. Lavarack and R. Cummings (Queensland Department of Environment and Heritage) for each site. Trees, shrubs and grasses were recorded in terms of their relative abundance (A-abundant, C-common, O-occasional, U-uncommon). An estimate was made of projective foliage cover (% of the sample site occupied by the vertical projection of foliage only, see McDonald et al., 1984) and the soil type noted. Nest sites of four individuals were described in more detail by P. Stumkat and I after the manner of Menkhorst et al. (1988). A square quadrat, centered on a frequently used denning tree, was defined with its apicies 30m to the N, S, E, and W (total area 1800m^2). Densities of trees were then presented as mean number of trees per 1000m^2. Within each quadrat all trees and shrubs

TABLE 1. Site and record details for *P. gracilis* sorted from the south by latitude. Age as adult (A) or juvenile (J). Sex as male (M) or female (F). Tenure includes National Park (N.P.)3 and State Forest (S.F.) +Site inside (east of) NP fence, but fence west of gazetted park boundary. * Record courtesy of J. Kehl, QFS.

FIG. 5. Comparison of size in four species of *Petaurus*. L to R, *P. gracilis* (adult male JM9014, Dalachy Creek), *P. abidi* (adult female M21664, Wilbeite, Papua New Guinea), *P. norfolcensis* (adult female J11514 Warwick), *P. breviceps* (adult female JM7396, Barretts Lagoon). Scale divisions in cm.

taller than 3m were identified, counted and their height and circumference-at-breast-height measured (Table 4).

Biochemical analysis

Frozen tissues of adult female JM8459 (Kennedy Valley) were the subject of electrophoretic allozymic analysis as described by Colgan & Flannery (1992).

SYSTEMATICS

Petaurus gracilis (de Vis, 1883)

Diagnosis

Petaurus gracilis is distinguished from *P. norfolcensis* by its larger size, reflected in the following measurements (in mm) for which respective values show no overlap:

Maximum skull length: mean 51.14, R= 49.80-52.60, N=7, SD=0.95 vs 45.33, R=40.96-49.05, N= 68, SD= 1.80.

Zygomatic width: mean 34.14, R=32.90-35.08, N=7, SD= 0.71 vs 30.15, R= 27.81-32.59, SD= 1.19.

Rostrum height: mean 14.02, R= 13.00-15.93, N= 9, SD= 0.84 vs 11.54, R= 9.89-12.68, SD= 0.62.

Tail-vent length: mean 353.50, R= 300-390, N= 10, SD=25.76 vs 239.43, R= 195-290, N= 30, SD=22.06.

P. gracilis has a significantly (P<0.001) narrower interorbital width than *P. norfolcensis*: mean 8.59, R= 7.30-9.82, N=9, SD= 0.95 vs 9.60, R= 7.97-11.73, N= 69, SD= 0.70.

P. gracilis is significantly (P<0.001) larger than *P. norfolcensis* in the following measures (Fig. 5):

Head-body length: mean 247.45, R= 215-265, N= 11, SD= 15.86 vs 200.72, R= 165-232, N= 29, SD= 17.17.

Hind foot length: mean 39.61, R= 37-43, N= 11, SD= 2.00 vs 32.03, R= 24-38, N= 29, SD= 3.01.

Weight: mean 349.45, R=255-410, N= 11, SD=39.69 vs 170.47, R= 110-301, N= 30, SD= 43.57.

Upper molar row length: mean 8.68, R=8.30-9.00, N= 9, SD= 0.21 vs 8.06, R= 7.37-8.90, N= 70, SD= 0.34.

Upper tooth row length: mean 23.90, R= 23.00-24.80, N=9, SD=0.51 vs 21.78, R= 19.76-23.51, N=69, SD= 0.84.

Lower molar row length: mean 9.43, R=9.00-9.91 N= 9, SD= 0.28 vs 8.73, R= 7.73-9.50, N= 69, SD= 0.34.

Upper incisor-premolar row length: mean 16.03, R= 15.47-16.59, N= 9, SD= 0.34 vs 14.46, R= 12.95-15.99, N= 69, SD= 0.69.

Rostral width between upper canines: mean 9.69, R= 9.10-10.30, N= 9, SD= 0.29 vs 8.67, R= 7.60-10.00, N= 69, SD= 0.46.

Width of ascending ramus: mean 13.13, R= 12.09-13.70, N= 9, SD= 0.32 vs 11.15, R= 9.93-12.50, N= 69, SD= 0.59.

Figs 6, 7 and 8 demonstrate the relationship between *P. gracilis* and *P. norfolcensis* for some of the measures refered to above.

Petaurus gracilis is distinguished from *P. breviceps* by its much larger size, reflected in the following measurements for which respective values show no overlap:

Maximum skull length: mean 51.14 vs 36.07, R= 33.17-37.91, N= 17, SD= 1.23.

Zygomatic width: mean 34.14 vs 24.79, R= 22.53-26.53, N=16, SD= 1.20.

Rostrum height: mean 14.02 vs 8.92, R= 8.29-9.55, N= 19, SD= 0.36.

Width of ascending ramus: mean 13.13 vs 8.18, R= 7.28-9.49, N= 20, SD= 0.56.

Tail-vent length: mean 353.50 vs 192.92, R= 159-235, N= 13, SD= 19.62.

Weight: mean 349.45 vs 93.09, R= 59-118, N= 11, SD= 19.19.

Upper molar row length: mean 8.68 vs 6.37, R= 6.05-7.75, N= 21, SD= 0.20.

TABLE 2. Queensland Museum specimens (prefixed JM) and tagged individuals caught and released (prefixed T). Age as adult (A), sub-adult (SA) or juvenile (J). Sex as male (M) or female (F). Measurements in mm, weight in g. Tail damaged as (d).

Regn #	Locality	Age	Sex	HB	TV	HF	E	Wt	Preservation	Colour phase & comments
JM5521	Mt Echo	A	M	260	365	38	25	—	skin, skull	measurements from old buff skins
JM5522	Mt Echo	A	M	255	340	33	25	—	skin, skull frag	
JM5523	Mt Echo	A	F	252	355	37	25	—	skin, skull frag	
JM7290	Barretts Lagoon	A	F	261	330	42	35	352	skin, skull spirit	buff
JM9729	Barretts Lagoon	J	F	58	60	12	8	—	spirit	hairless young of JM7290
JM9730	Barretts Lagoon	J	F	48	59	11	8	—	spirit	hairless young of JM7290
JM7400	Barretts Lagoon	A	M	265	335	43	36	410	skin, skull, spirit	buff
JM8549	Kennedy Valley	A	F	240	270(d)	38	33	350	spirit	buff
JM8550	Kennedy Valley	J	F	95	121	20	15	43	spirit	buff, pouch young of JM8549
JM9014	Dalachy Ck	A	M	249	354	41	35	350	skin, skull, frozen body	dark
JM9015	Porters Ck	A	F	264	360	40	32	407	skin, skull, frozen body	
JM9016	Murray Upper	A	F	256	346	41	33	370	skin, skull, frozen body	'aberrant' phase
T4026	Barretts Lagoon	A	F	220	300	37	29	345		dark, caught in den 22.02.91
T4027	Barretts Lagoon	SA	F	200	320	32	31	195		dark, caught in nest box #8 10.05.91
T4028	Barretts Lagoon	SA	F	180	330	35	-	215		dark, caught in nest box #8 10.05.91
T4029	Barretts Lagoon	A	F	250	390	38	27	255		buff, caught while feeding 19.05.91
T4030	Barretts Lagoon	A	M	247	380	38	29	330		buff, caught in den 05.08.91
T4031	Barretts Lagoon	A	F	215	380	37	34	325		buff, caught in den 08.08.91
T4032	Barretts Lagoon	J	M	120	165	26	17	65		buff, nestling of T4026 26.11.91
T4033	Barretts Lagoon	J	F	120	175	24	17	69		buff, nestling of T4026 26.11.91

Upper tooth row length: mean 23.90 vs 16.90, R= 16.04-17.93, N= 20, SD= 0.54.

Lower molar row length: mean 9.43 vs 6.99, R= 6.60-7.91, N= 21, SD= 0.28.

Upper incisor-premolar row length: mean 16.03 vs 11.05, R= 10.24-12.14, N= 20, SD= 0.48.

Rostral width between upper canines: mean 9.69 vs 6.79, R= 6.29-7.30, N= 20, SD= 0.31.

Petaurus gracilis is immediately distinguished from *P. abidi* by the atrophied condition of P^2 in *gracilis*, but which, in *abidi*, is well developed and subequal in crown height to both P^1 and P^3. *P. gracilis* is further distinguished by its reduction in buccal ectoloph enamel on M^2 and M^3 and by the reduction in the paracone relative to the metaconule (the posterolingual cusp previously and commonly termed the hypocone; see Woodburn et al., 1987: 641 for discussion) in M^2. *P. gracilis* is also distinguished from *P. abidi* by its smaller dimensions in the following measurements for which respective values show no overlap:

Interorbital width: mean 8.59 vs 10.42, R=9.70-11.50, N= 3, SD= 0.78.

Upper molar row length: mean 8.68 vs 9.50, R= 9.30-9.70, N= 2, SD= 0.21.

Petaurus gracilis is distinguished from *P. australis* by its smaller size, reflected in the following measurements (for which respective values show no overlap:

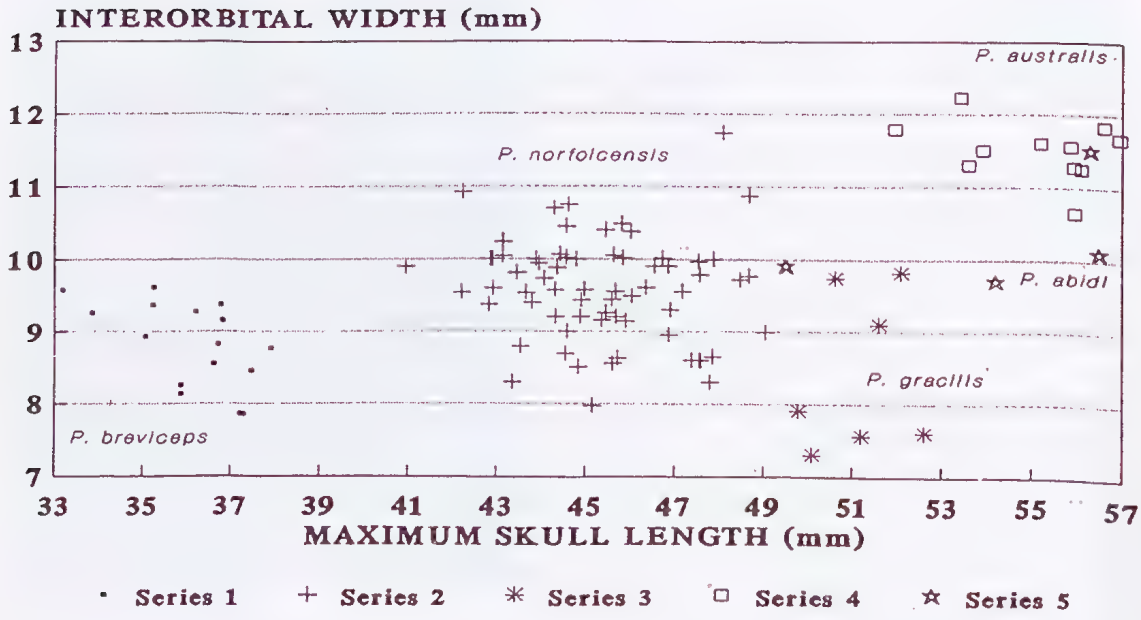
Zygomatic width: mean 34.14 vs 37.38, R= 34.98-39.70, N= 10, SD= 1.45.

Tail-vent length: mean 353.50 vs 433, R= 410-460, N= 6, SD= 17.88.

Interorbital width: mean 8.59 vs 11.51, R= 10.65-12.22, N= 11, SD= 0.38.

Rostral width between upper canines: mean 9.69 vs 12.00, R= 11.06-12.70, N= 11, SD= 0.53.

Ear length: mean 31.96, R= 27-36, N= 10, SD= 2.85 vs 51.40, R= 46-56, N= 5, SD= 3.88.



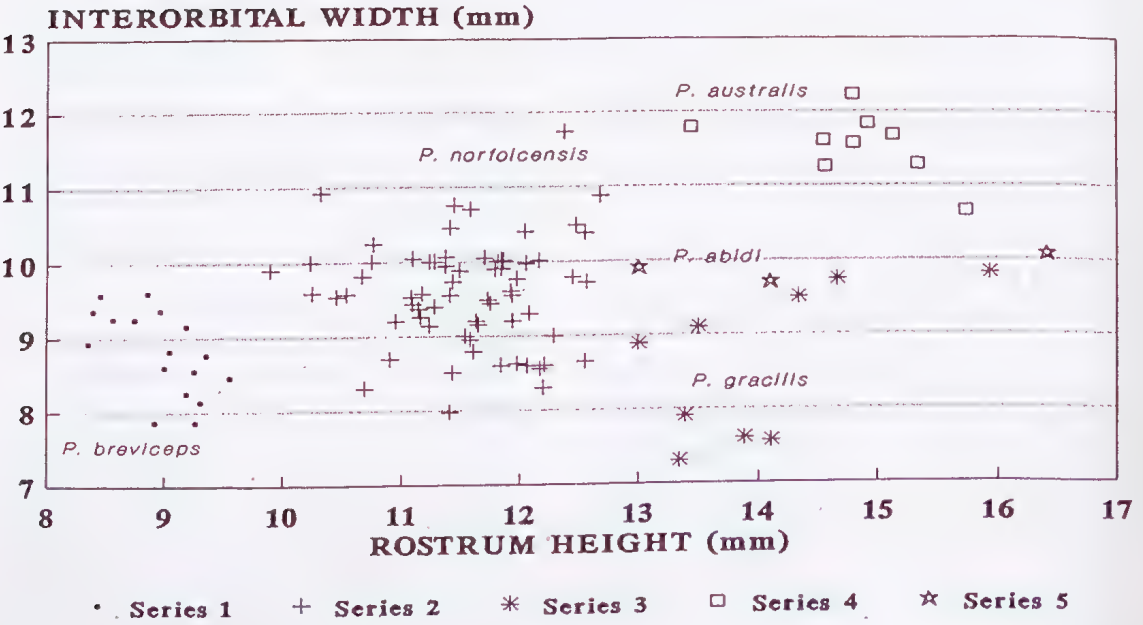
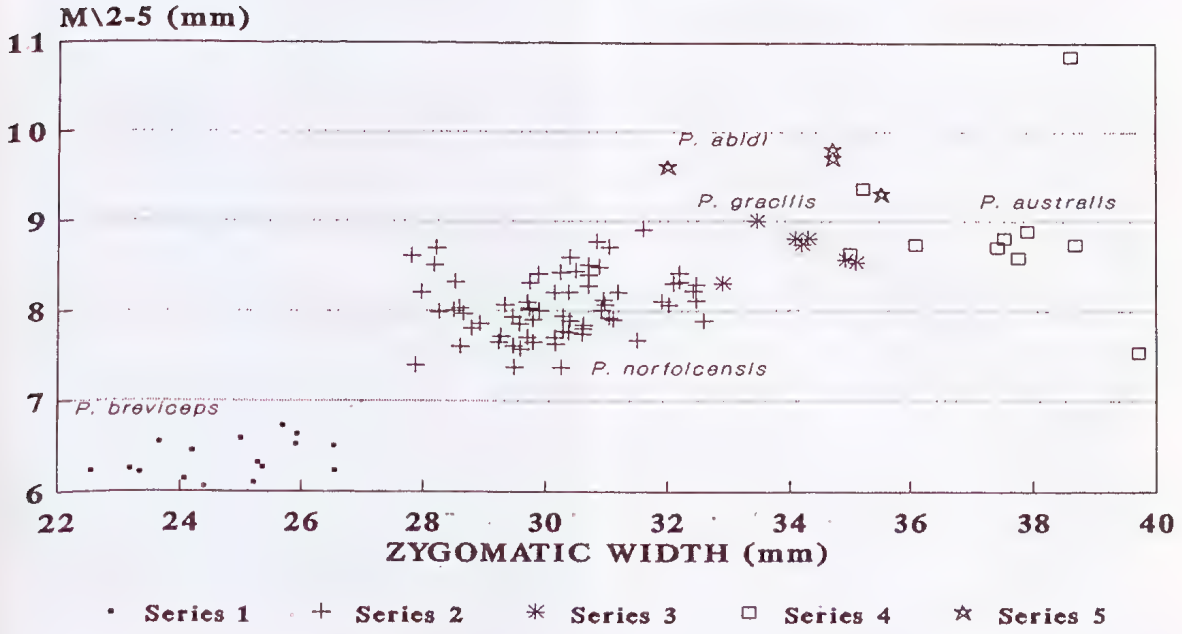


FIG. 6. Bivariate plots of interorbital width against rostrum height and maximum skull length. Series 1= *P. breviceps*, Series 2= *P. norfolcensis*, Series 3= *P. gracilis*, Series 4= *P. australis*, Series 5= *P. abidi*.



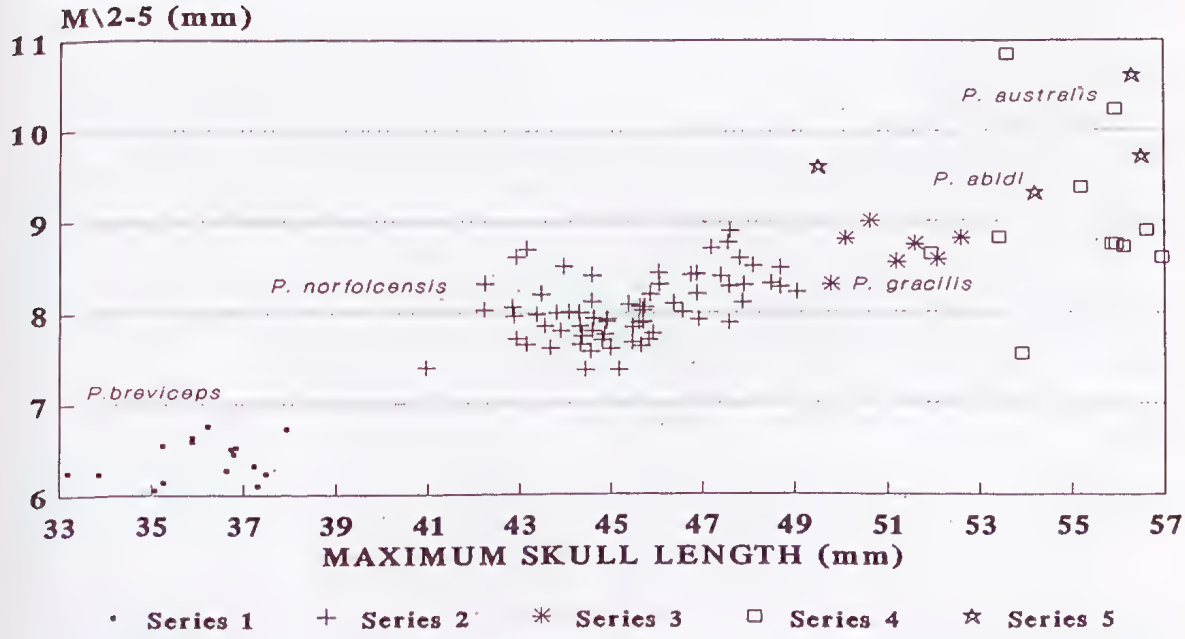
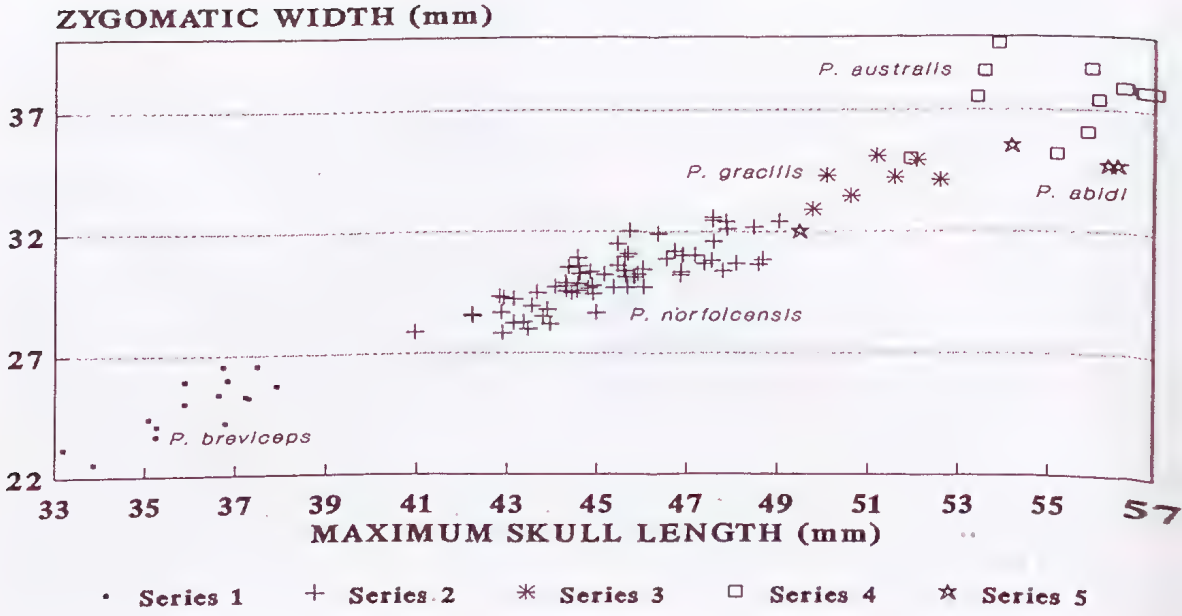


FIG. 7. Bivariate plots of upper molar row (M\2-5) against zygomatic width and maximum skull length. Series 1= *P. breviceps*, Series 2= *P. norfolcensis*, Series 3= *P. gracilis*, Series 4= *P. australis*, Series 5= *P. abidi*.



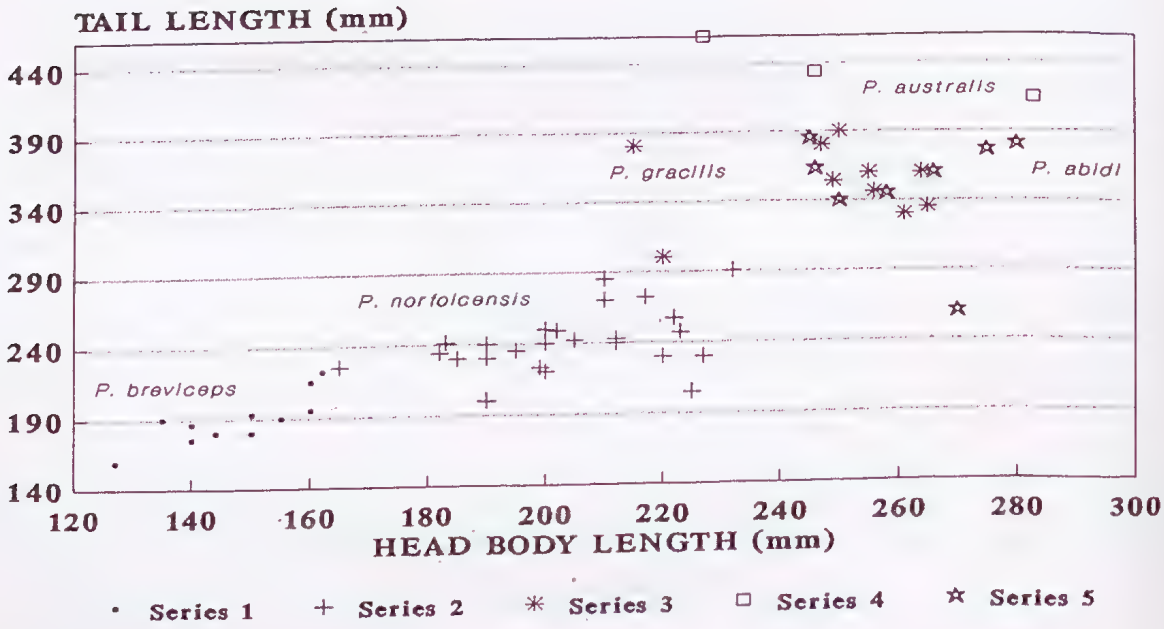


FIG. 8. Bivariate plots of zygomatic width against maximum skull length, and head body length against tail length. Series 1= *P. breviceps*, Series 2= *P. norfolcensis*, Series 3= *P. gracilis*, Series 4= *P. australis*, Series 5= *P. abidi*.

FIG. 9. Dorsal perspective of three colour morphs in *P. gracilis*. L to R, dark phase (adult male JM9014), buff phase (adult female JM9015), aberrant phase (adult female JM9016).

DESCRIPTION

Externally, this species of *Petaurus* is distinctive for its large size, long, relatively short-haired tail and buff to mahogany-brown belly (Figs 5, 9, 10). There is considerable variation in the depth of both dorsal and ventral tonings and the band of fur along the lateral anterior edge of the gliding membrane may be buff, rich orange or deep mahogany. Ventral fur (adult and sub-adult of both sexes) may be either buff, honey-yellow or deep mahogany (Figs 9, 10; Table 2).

Pelage: Colours (where capitalised after Ridgway, 1912) of the buff phase (example used JM7400) are as follows: Fuscous-Black mid-dorsal head-and-body stripe variable in width (partially depending on the 'lie' of the body fur) commencing at a point between the anterior edge of the eyes and extending posteriorly to the rump. It is 12mm wide between the ears, 5.6mm at mid-neck, 17mm at mid-shoulder blades and fading away over the rump. Fur of the mid-back (16.3mm long) with basal 14.4mm Smoke Gray, median 1.4mm either Pale Smoke Gray (off-white) or Chamois (brown-yellow), apical 0.5mm Fuscous-Black. The back therefore appears overall a patchy wash of smoky grey (Smoke Grey) and yellowish-brown. The yellowish patches are most pronounced over the shoulders, along the flanks and over the rump. Medially thickened Fuscous-Black-tipped guard hairs are interspersed very sparsely through the fur and are 20.4mm on the mid-back and reduce to 3.6mm on the tip of the snout where they are entirely Fuscous-Black. Fur on either side of the head-stripe is Pale Smoke Gray with a yellowish-buff wash. A ring of Fuscous-Black fur encircles the eye, and fur below the eye-ring to the corner of the mouth is Pale Olive-Buff. Muzzle (delineated by the presence of mystacial vibrissae) a weak Fuscous-Black. Fuscous-Black fur encircles the dorsal posterior and ventral base of the pinna, extending forward and down to slightly posterior of the genal vibrissae. Directly anterior to the ear and posterior to the genal vibrissae, is a patch of anteriorly-directed Pale Olive-Buff fur. The pinna is virtually naked on the inner surface, and on the distal 11mm of the outer surface. The pinnae of living animals are a pink-bronze. A patch of pale Olive-Buff fur (hairs up to 8mm long) on the posterior external edge of the pinna forms a conspicuous tuft.

Dorsally, the patagium is fringed along its length by a thickly-furred band of Cream-Buff fur (hairs 3mm long). Midway between the wrist and digit 5, the apex of a triangular patch of striking Chamois-coloured fur extends in a narrowing band (to 5mm wide) posteriorly along the inner side of the outermost Cream-Buff band. More mesially, and slightly overlaying the Chamois band the patagium is coloured Sepia in a hard line 6mm wide and extending posteriorly from the wrist to the ankle. Sepia fur sparsely covers the rest of the patagium.

Ventrally, the patagium is fringed in a 5mm wide band of Clay coloured fur from the claw of digit 5 to the ankle. More mesially this band is partly overlaid by another 5mm wide band of Sepia which extends from 20mm posterior of the digit 5 claw to the ankle where its colour fades. The bulk of the patagium is then sparsely covered with 15mm long Honey-Yellow fur.

The soft ventral fur (18mm long on the belly) is Cream-Buff to Honey Yellow, but is suffused with Smoke Gray hairs on either side of the neck and around the muzzle.

Forefeet digits are thinly covered with Smoke Gray hairs. Hindfeet are more thickly covered with slightly lighter Pale Olive-Buff which contrasts with a 'mitten' of Smoke Gray over the metatarsals extending up to the inner posterior region of the thigh in a triangular stripe 23mm at

TABLE 3. Localities surveyed, spotlight effort and arboreal mammals recorded. Mammals are grouped by locality, not by date. Fruit bat presence not recorded.*Observed on dry *E. acmemoides* ridge. # Observed at approx. 610 m. a.s.l. ▲ Site cleared Feb 1990.

SURVEY AREA		Lat.	Long.	PERIOD	SPOTLIGHT MANHOURS	ARBOREAL SPP OBSERVED (N)
1. Bluewater		19°13-14'S	146°25-30'E	May 92	8	—
2. Rollingstone	Clemant S.F. west	19°05-06'S	146°25-27'E	May 92	13	*P.breviceps* (3+1 call)
				Jun 92	2	
	Clemant S.F. east	19°04-05'S	146° 25-27'E	May 92	16.5	*P.breviceps* (1) *T.vulpecula* (3)
				Jun 92	3	
				Sep 92	13.5	
3. Paluma turnoff		18°58'-59'S	146 °17-18'E	May 92	2	—
				Jun 92	7	
4. Amos Rd- coast- Crystal Ck		18°54-57'S	146°16-17'E	May 92	8	*T.vulpecula* (1)
5. Orient Ck		18°47-48'S	146°13-14'E	Sep 92	26	*T. vulpecula* (2)
6. Ashton Ck		18°37-38'S	145°53-56'E	Jun 92	18	*P. gracilis* (3) *T. vulpecula* (8)* *P. breviceps* (1)*
7. Lannercost Ck		18°37'S	145°56-58'E	Jun 92	6	*P. gracilis* (1)
8. Wallaman Rd		18°37'S	145°52-53'E	May 91	10	—
				Mar 92	1	
9. Manor Ck		18°29'S	146°03'E	Jun 92	15	*P. breviceps* (1)
10. Elphinstone Ck		18°29'S	146°01'E	Mar 92	4	*P. gracilis* (1)
11. Porters Ck		18°26'S	146°07'E	Mar 92	9	*P. gracilis* (2)
				May 92	9	
12. Mullers Ck		18°26'S	146°07'E	May 92	12	*P. gracilis* (2)
13. Yamanie N.P. Mt Echo		18°24-25'S	145°46-47'E	Jun 86	24	*P. gracilis* (1)
				Jul 88	18	
				Mar 92	6	
14. Henrietta Holding		18°24'S	145°45'E	Oct 92	11	—
15. Gowrie Ck		18°23-24'S	145°50'E	Jul 88	12	*P. volans* (1)
16. SE of 5 mile Ck		18°20-23'S	146°03-06'E	May 92	10	—
17. SW of 5 mile Ck		18°20-23'S	146°03-06'E	May 92	28	—
18. Macalister Mts		18°17-19'S	145°57-58'E	Jul 88	70.5	*D. lumholtzi* (1) *P. herbertensis* (4) *P. breviceps* (1)
19. Ellerbeck Rd		18°14'59"S	145°58'36"	Nov 92	2	*P. breviceps* (1)
20. Hinchinbrook Is		18°14'S	146°08'E	Sep 92	16	*U. caudimaculatus* (1)
21. Baird Ck		18°12'S	145°58'E	Mar 92	2	*P. gracilis* (1)
22. Kirrima-Blencoe Falls		18°09-14'S	145°32'-38'E	Mar 92	11	*T. vulpecula* (28) # *P. volans* (26) # *P. peregrinus* (11) # *P. breviceps* (2)# *A. pygmaeus* (1)#
23. Edmund Kennedy N.P.		18°08-11'S	145°58-59'E	Sep 91	31.5	*P. gracilis* (2 calls) *D. trivirgata*
				Mar 92	27	
24. Dalachy Ck		18°08-09'S	145°56-57'E	Mar 92	15.5	*P. gracilis* (3) *T. vulpecula* (2) *P.breviceps* (1)
25. Murray Upper		18°08'S	145°47'E	Mar 92	3	*P. gracilis* (1)
26. North Murray		18°05-06'S	145°46-48'E	Mar 92	11	—
27. Yingalinda Beach		18°03'S	145°59'E-146°02'E	May 91	20	*P. gracilis* (1)
				Aug 91	24	
				Nov 91	16	

TABLE 3 cont. Localities surveyed, spotlight effort and arboreal mammals recorded.

SURVEY AREA	Lat.	Long.	PERIOD	SPOTLIGHT MANHOURS	ARBOREAL SPP OBSERVED (N)
28. Barretts Lagoon to Bedford Ck	18°02-04'S	145°58-59'E	Dec 89	36	*U. caudimaculata* (1) *D. trivirgata* (2) *P. breviceps* (1)
			Feb 91	46	
			May 91	15.5	
			Sep 92	9	
29. ▲ Barretts Lagoon (southwest bank)	18° 02'S	145°58'E	Dec 89	115	*P. gracilis* (9) *P. breviceps* (6) *D. trivirgata* (1) *A. pygmaeus* (2)
30. Barretts Lagoon (northeast bank)	18° 02'23"S	145°58'46"E	Sep 91	1	*P.gracilis* (1 + 1 call)
31. Barretts Lagoon ("Ricefields")	18°01'S	145°58'E	Feb 91	110	P. gracilis (10) *P. breviceps* (4) *D. trivirgata* (1)
			May 92	68	
			Aug 91	249	
			Nov 91	18	
			Mar 92	5.5	
32. Barretts Lagoon (east)	18°01'S	145°59'E	May 91	10	*P.gracilis* (9 + 2 calls) *P. breviceps* (3) *A. pygmaeus* (1)
			Aug 91	17	
			Nov 91	20	
			Mar 92	5.5	
			Sep 92	9	
33. Hull R	17°58'S	146°01-02'E	Oct 92	8	*P. gracilis* (1)
34. Mission Beach Rd	17°55-56'S	146°00-05'E	Oct 92	23	*D. trivirgata* (1)
35. Graham Ra N.P.	17°18-19'S	146°01'E	Oct 92	15	—
36. S of Daintree R, Mossman	16°17-18'S	145°25-26'E	Oct 92	12	—
			TOTAL	1334	

its widest point almost to the base of the tail. A similar, but darker forearm 'stripe' (Fuscous Black) extends from the base of digit 1 along the antero-mesial region of the forearm to terminate in a 20mm wide patch at the base of the forearm.

The tail is thinly haired and approximately one-and-a-half times longer (average 147%) than the head and body length. Near its base (40mm from the body) the fur is slightly shorter dorsally (25mm) and ventrally (17mm) than laterally (33mm). 40mm from the tip of the tail the fur is even in length and slightly shorter (24mm). The distal one-third of the tail is Fuscous Black changing reasonably abruptly to honey-grey (basal 20mm Smoke Gray, apical 13mm Chamois).

Males exhibit naked, ovoid glandular patches on the crown of the head within the black head-stripe (gland approx. 9mm × 5mm) and at the base of the throat (approx. 9mm × 7mm).

Vibrissae: Approximately 16 relatively short Fuscous Black mystacial vibrissae occur on each side and measure up to 19mm long; supra-orbital vibrissae (Fuscous Black) number approx. 2 each side, genals number 2-3 (Fuscous Black) and metatarsals number 4 (Chamois).

Claws of fore and hind feet are relatively large with maximum chord length of digit 4 and 5 claws approx 9mm. Digit 4 is the longest digit of manus or pes and digit 4>5>3>2>1.

In the dark phase (Figs 9, 10), white and buff colours are replaced with deep gingers, browns or Fuscous-Black. The pattern of body stripes, tail and limb 'pennants' is as in the buff form but the median section of mid-back varies from Tawny Olive to Deep Mouse Gray (not Pale Smoke-Gray), the head may be Tawny Olive to Pale Olive Gray, the cheeks and flanks Honey Yellow to Dark Olive-Gray (not Pale Olive-Buff), and the dorsal anterior flange of the patagium Honey Yellow to Deep Olive Yellow (not Chamois). The dorsal surface of the patagium is Deep Mouse Gray, its external margin Deep Olive-Gray, ventrally the patagium is fringed in a 5mm wide band of Deep Olive-Gray fur tipped with buff (the apical 1mm) from the claw of digit 5 to the ankle. More mesially this band is partly overlaid by another 5mm wide band of Fuscous-Black which extends from 20mm posterior of the digit 5 claw to the ankle where its colour fades. The bulk of the patagium is then sparsely covered with Deep

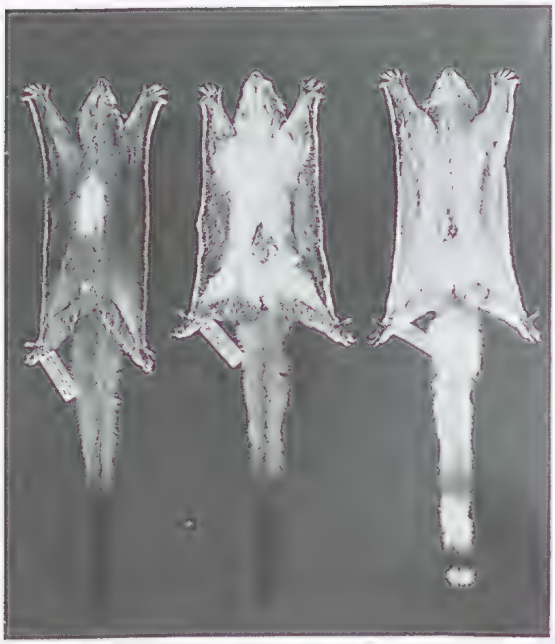


FIG. 10. Ventral perspective of three colour morphs in *P. gracilis*. L to R, dark phase (adult male JM9014), buff phase (adult female JM9015), aberrant phase (adult female JM9016).

Olive-Gray fur. Fur encircling the dorsal posterior and ventral base of the pinna, extending forward and down to slightly posterior of the genal vibrissae is Fuscous-Black. The ventral surface from throat to sternum is a Grayish Olive to Tawny Olive darkening to Sepia or Dark Olive near the belly. A small spot or streak of white fur may be present on the belly, sternum or slightly anterior to the pouch. The scrotum is buff-coloured, and hair inside the pouch Warm Sepia.

Aberrant form (Figs 9,10): JM9016 may represent an aberrant form where the ventral surface is more richly coloured with Clay Colour (orange-ochre) fur which extends around the forefeet up to the elbows, around the hind feet as far as the knees, and over the patagial edges to end along the animal's flanks . A small white patch of fur is present in the head-and-body stripe just posterior the ears. The tail is banded as follows (from the base), 11mm white, 14mm Mineral Gray, 50mm Tilleul Buff, 36mm Mineral Gray, 40mm Tilleul Buff, 57mm Mineral Gray, 26mm Fuscous (marking the proximal extent of a normal black tail-tip), 64mm Pale Olive-Buff, 40mm Fuscous-Black. Alexander (1981) illustrated an aberrant specimen, M8134, from Grafton, New South Wales similar to JM9016. He commented on the possibility of M8134 being 'some sort of hybrid' between *P. breviceps* and *P. norfolcensis*. Given the size disparity between *P. breviceps* and *P. gracilis* and the observed intolerance of *P. gracilis* toward *P.breviceps* in the field, the likelihood of JM9016 representing a hybrid is probably remote.

Cranium and dentition: Essentially similar to *P. norfolcensis* except skull longer and much broader, with a much higher rostrum and wider ascending ramus. In spite of such consistently high values in *P. gracilis*, upper molar row lengths are not significantly longer than those of large examples of *P. norfolcensis*, and interorbital length in *P. gracilis* is significantly narrower than *P. norfolcensis* of all sizes (Figs 6-8).

Biochemical analysis: Electrophoretic allozymic analysis conducted by Colgan and Flannery (1992) showed *P. gracilis* to be genetically distinct (three fixed differences; adenylate kinase (1), glycerophosphate dehydrogenate and phosphoglucomutase in 21 loci) from *P. norfolcensis norfolcensis* (Limeburners Creek, NSW).

DISTRIBUTION

P. gracilis has been recorded only from a narrow band of medium to low woodland on Quaternary coastal alluvium and granite north of Wharps Holding (S of Herbert River, Ingham) to the Hull River, a latitudinal range of almost 80km (Fig. 1). In this band, *P. gracilis* has been found at altitudes below 90m a.s.l. with most records from between the 0-20m contours (Tables 1 and 2).

RESULTS

HABITAT

Vegetation associated with *P. gracilis* included Vegetation Types 15a (Medium Open-forest i.e. paperbark swamp), 17 (Coastal Beach Ridges and Swales), 19 (Coastal Floodplains and Piedmont slopes), 20 (Texture-contrast Soils with Impeded Drainage on Coastal Plains) and 24 (Cleared) of Tracey (1982). The appropriate Tracey vegetation type (TVT) appears with each site vegetation proforma below. The following abbreviations were used to describe the relative abundance of plant species (A-abundant, C-common, O-occasional, U-uncommon).

Sites marked thus * indicate records supplied courtesy of Queensland Forest Service. Tracey (1982) provides an overview of climate, physiography, geography and soils of the area. The Quaternary lowland coastal plains and extensive

beach ridges which typify the distribution of *P. gracilis* occur in narrow corridors up to 10km wide and 50km long between the steep ranges near the coast and the main scarp further upland. Soil types are determined by drainage; on the better-drained levees yellow friable loams predominate, and there is a progression to gleyed podzolic soils, humic gleys and acid peats as the site drainage becomes poorer. Calcareous or siliceous sands are found on the younger near-coastal ridges and podzols occur on the older ridges.

Annual rainfall is high, but widely different rainfall regimes operate and vary considerably over short distances because of local topographic changes which include the height and orientation of mountain ranges and the direction of the coastline with respect to the prevailing south-east air stream. The wide coastal plains and beach ridges show dramatic drops in rainfall from coast to foothills, e.g. Halifax 2127mm west to Upper Stone 1533mm in 45km. The relative dryness of foothills and eastern slopes may account for the apparent restriction of the glider to areas of very low elevation (below 90m a.s.l.). While foothills may receive only slightly less summer rainfall than coastal plains (Rollingstone, 19°03'S 146°24'E, Dec 220mm, Jan 416mm, Feb 344mm compared with coastal plain Euramo, 18°00'S 145°56'E Dec 167mm, Jan 597mm, Feb 652mm), dry season rainfall in foothills may be inordinately low (Rollingstone Jun 15mm, Jul 11mm, Aug 18mm, Sept 25mm contrasted with Euramo Jun 132mm, Jul 93mm, Aug 67mm, Sept 99mm). Latitudinal variation in rainfall may also be dramatic over short distances, e.g. Tully 4188mm south to Cardwell 2132mm in 40km.

SITE RECORDS (see Table 1)

Two historic records exist for which there can be no precise fix:

i. 'North of Cardwell' (de Vis 1883). No habitat information is included in the original description, and to date no Broadbent diary has been found for that period. The Edmund Kennedy National Park (NP 771) now accounts for approximately 6200ha of largely unaltered lowland coastal land immediately north of Cardwell (to the Murray River). The park contains a variety of lowland vegetation communities (all below 20m elevation) from mangroves, bulkuru swamps, paperbark forest and dry eucalypt woodland through to rainforest. Approximately 30% of this park could be considered possible habitat for *P. gracilis* (open sclerophyll forest with shrubby understorey), approximately 1% could be considered optimal habitat. The glider has recently been recorded within the park boundary. For more detailed floristics see habitat data (for sites 13 and 14) below.

ii. 'Mt Echo' (locality information on tags attached to skins JM5521, JM5522, JM5523). No specific vegetation or elevation information is available with this record and although the 1886 diary of Kendall Broadbent documents his camp on the Herbert River and his collecting efforts on the steep slopes and summit of Mt Echo, no details are given concerning where gliders were collected. The problem is further compounded by Broadbent's various references to vernaculars such as 'small flying squirrels', 'flying squirrels', and a 'large flying squirrel' in lieu of specific titles for collected examples of *Petaurus breviceps*, *P. gracilis* and *Petauroides volans*. Vegetation of the dry slopes of Mt Echo beside the Herbert R has probably changed little since Broadbent's day. At one site (18°24'52"S 145°46'13"E) the dominant species in the upper canopy (23m with 30% cover) were *Eucalyptus tereticornis* (C), *Lophostemon suaveolens* (A), *E. clarksoniana* (O) and *E. tessellaris* (O). Understorey (<5% cover) species comprised *Planchonia careya* (O) and *Pandanus* sp. (O). Ground layer (100% cover) consisted of *Imperata cylindrica*, *Mnesithea rottboellioides* (A), *Trumfetta rhomboidea* (C) and *Panicum maximum* (O). Soil was rocky, brown sandy loam, TVT 19.

Contemporary records for which more precise fixes are available (Fig. 1):

1. ***Wharps Holding** (18°41'18"S 146°04'25"E). Dominant species of the upper stratum (25m with <45% cover), *E. platyphylla* (U) and *Melaleuca dealbata* (A). Understorey (20% cover) composed of *L. suaveolens* (C) and *Pandanus* sp. (U). Ground layer (50% cover and heavily grazed) probably *I. cylindrica* and other grasses. This area was notable for its coarse mosaic of single species associations. Isolated clumping of single species included *M. dealbata*, *L. suaveolens*, *E. tessellaris* and *Acacia crassicarpa* with *E. platyphylla* scattered throughout. This area is renown for its protracted periods of extensive inundation during the wet season. Soil, grey loam, TVT approaching 16p. A second glider observation was made nearby (100m N) on a gently sloped rocky ridge (40m a.s.l.) where dominant species of the upper stratum (18m with <30% cover) included *E. platyphylla* (O), *L. suaveolens* (A), *E. tessellaris* (O) and *E. dolichocarpa*. The understorey (<1% cover) was com-

TABLE 4. Species, numbers, dimensions and densities of trees at four *P. gracilis* nest sites . CBH=circumference at breast height.

Nest Site	Total No. trees	Tree species	Number on grid (% of all trees)	Mean number /1000 m^2	Height range (m)	Mean Ht (m), (SD),(SE)	CBH range (mm)	CBH mean, (SD),(SE)
1. Barretts Lagoon 18°01'33"S, 145 59'08"E *E.intermedia* (live) Ht 7m,CBH 780mm Surveyed 13.8.91 Fig. 11.	1204	*Eucalyptus intermedia*	31 (2.6)	17.2	3-10	7.10 (2.13) (0.69)	160-940	554.61 (224.32) (7.24)
		E. pellita	1 (0.08)	0.5	10	10.00	730	730
		Lophostemon suaveolens	26 (2.2)	14.4	3-9	6.11 (2.23)(0.09)	110-920	447.69 (254.36) (9.78)
		Acacia crassicarpa	21 (1.7)	11.7	3-8	4.76 (1.58) (0.07)	110-650	252.86 (154.89) (7.38)
		A. flavescens	3 (0.2)	1.7	3	3.00	100-130	113.33 (15.27) (5.09)
		A. pubirhachis	1 (0.08)	0.5	3	3.00	100	100
		Melaleuca viridiflora	69 (5.7)	38.3	3-8	4.23 (1.41) (0.02)	70-670	270.88 (154.01) (2.23)
		Pandanus citraceus	34 (2.8)	18.9	<1			
		Xanthorrhoea johnsonii	1018 (84.5)	565.5	<1			
2. Barretts Lagoon *Scleria* swamp 18°01'44"S 145°59'04"E *E. pellita* (live) Ht 12m,CBH 1490mm Surveyed 14.8.91 Fig. 12.	466	*E. pellita*	17 (3.6)	9.4	3-13	9.00 (4.05)(0.24)	110-1650	709.41(560.03) (32.93)
		L. suaveolens	52 (11.2)	28.9	3-14	6.79 (3.52) (0.07)	130-1590	501.35 (384.82) (7.40)
		A. crassicarpa	4 (0.9)	2.2	5-12	7.25 (3.20) (0.80)	200-460	370.00 (197.15) (49.29)
		A. flavescens	1 (0.2)	0.5	3	3.00	110	110
		M. quinquenervia	176 (37.8)	97.8	3-14	8.68 (3.65) (0.02)	110-1940	513.01 (304.86) (1.732)
		Melicope elleryana	3 (0.6)	1.7	3	3.00	100-150	120.00 (26.46) (8.82)
		Deplanchea tetraphylla	1 (0.2)	0.5	12	12.00	780	780
		P. citraceus >1m	19 (4.1)	10.5	2-10	5.89 (2.86) (0.15)	430-650	542.63 (65.22) (3.43)
		P. citraceus <1m	43 (9.2)	23.9	<1			
		Gahnia sieberiana	131 (28.1)	72.8	<3			
		X. johnsonii	18 (3.9)	10.0	<1			
		Banksia integrifolia	1 (0.2)	0.5	6	6	470	470
3. Barretts Lagoon "Ricefields" 18°01'26"S 145°58'46" E *L. suaveolens* (live) Ht 10m, CBH 1250mm Surveyed 15.8.91 Fig. 13.	690	E.intermedia	18 (2.6)	10.0	3-12	7.00 (2.30) (0.13)	120-840	408.89 (205.57) (11.42)
		E.pellita	37 (5.4)	20.5	3-15	6.89 (3.93) (0.11)	70-3000	589.02 (760.50) (20.55)
		L. suaveolens	73 (10.6)	40.5	3-10	5.49 (2.10) (0.03)	60-1400	375.30 (305.34) (4.18)
		M. viridiflora	6 (0.9)	1.7	3-6	4.33 (1.03) (0.17)	90-550	241.67 (149.45) (24.91)
		M. dealbata	1 (0.1)	0.5	6	6.00	300	300.00
		A. crassicarpa	11 (1.6)	6.1	3-9	6.36 (1.80) (0.16)	80-700	428.18 (200.64) (10.61)
		A. flavescens	2 (0.3)	1.1	3-4	3.5 (0.70) (0.35)	150-180	165.00 (21.21) (10.61)
		Planchonia careya	1 (0.1)	0.5	4	4.0	210	210.00
		P. citraceus >1m	15 (2.2)	8.3	2-6	3.93 (1.03) (0.07)	280-450	350.00(50.00)(3.33)
		P. citraceus <1m	272 (39.4)	151.1	<1			
		X. johnsonii	245 (35.5)	136.1	<1			
4.Barretts Lagoon 10°01'35"S 145°58'52"E Dead stag Ht 13m, CBH 1620mm Surveyed 16.8.91 Fig. 14.	680	*E. intermedia*	38 (5.6)	21.1	3-14	8.45 (3.29) (0.09)	70-1940	509.21 (370.20) (9.74)
		E. pellita	29 (4.3)	16.1	3-14	7.65 (3.99) (0.14)	50-1040	425.51 (344.78) (11.89)
		L. suaveolens	51 (7.5)	28.3	3-12	5.84 (2.65) (0.05)	90-10000	293.92 (205.76) (4.03)
		M. dealbata	2 (0.3)	1.1	2-4	7.00 (4.24) (2.120)	130-520	325.00 (275.77) (137.89)
		A. crassicarpa	33 (4.8)	18.3	3-10	6.00 (2.60) (0.08)	60-670	284.54 (188.65) (5.72)
		A. flavescens	27 (4.0)	15.0	3-12	7.15 (2.75) (0.10)	60-740	328.15 (199.19) (7.38)
		P. careya	2 (0.3)	1.1	3-4	3.50 (0.71) (0.35)	200-240	220.00 (28.28) (14.14)
		P. citraceus >1m	3 (0.4)	1.7	2-6	4.67 (2.31) (0.77)	320-490	406.67 (85.05) (28.35)
		P. citraceus <1m	84 (12.3)	46.7	<1			
		X. johnsonii	411 (60.4)	228.3				

Additional notes on nest sites of Table 4.
Understorey.

Site 1 (Fig. 11): Dry low woodland between swales with groundcover species homogeneous throughout site. 70-95% cover and dominated by *Themeda triandra* and *Leptocarpus ramosus* (both about 1 m) with smaller representation (< 10 specimens) by *Lomandra longifolia*, *Dianella caerulea*, *Melastoma affine*, *Banksia integrifolia* var. *aquilina*, *Dipodium ensifolium*, *Schoenus sparteus* and *Lindsaea ensifolia*. Regrowth (< 3 m) with 10-20% cover by *Acacia mangium*, *A. crassicarpa*, *Lophostemon suaveolens*, *E. pellita*, *M. viridiflora* and *A. pubirhachis*. Of *X. johnsonii*, (tallest 800mm), 32 with green scapes (7 with *P. gracilis* foot prints, 2 with gouges), 130 with dry seeded scapes. Site 1 sufficiently elevated to escape inundation in wet season.

Site 2 (Fig. 12): Tall teatree-razorgrass swamp with eastern edge encroaching swale and dominated by dense groundcover (90%) of *Leptocarpus ramosus*, *Blechnum indicum*, *Scleria ciliaris*, *Baumea* sp., and *Ischaemum australe* var. *villosum*. Sparce cover of *M. affine*. Southern and western quarters dominated by *S. ciliaris* and *B. indicum* to 1400mm (70-90%), *Baumea* sp. (approx 2%) and *Dichranopteris linearis* (approx 5%). The drier, more elevated western quarter dominated by *I. australe* var. *villosum* and *L. ramosus* at 400mm (approx 50%) with *Gahnia sieberiana* at 1.2m (10%), *D. linearis* at 600mm (5%) and stunted *M. quinquenervia* (2%) with *L. ramosus* at 600mm and *Erocaulon australe* at 300mm in the swale. Sparse (<1%) regenerating vegetation comprised *M. quinquenervia* in western, southern and eastern quarters with *A.crassicarpa, A.flavescens* and *L. suaveolens* (total 2%) in the north. *X. johnsonii* showed 4 green scapes, 4 dry seeded scapes, 1 with foot prints and 0 scarred.

Site 3 (Fig. 13): Swale and medium to low woodland. Southern half (swale) dominated by dense groundcover (75% cover) of stunted *M. quinquenervia* (5-6%) at 0.5m, *M. viridiflora* (30 specimens all < 3 m), *I. australe* var. *villosum* (80%) at 1.1 m, *Themeda triandra* (1-5%), *Leptocarpus ramosus* (5%), *Scleria polycarpa* (5%) and *Eriachne triseta* (5%). Northern half (woodland) densely covered (100%) with *I. australe* var. *villosum*, *T. triandra* and *Lomandra longifolia*, *Smilax australis* abundant and up to 4 m, *L. ensifolia* common in localised clumps, *M. affine* sparse, *D. caerulea* common, *Planchonia careya* common and up to 3 m, *M. affine* to 2m but uncommon, *Schoenus calostachyus* common. Revegetation dominated by *A. flavescens* to 3m and spaced at approximately 2 m, *A.crassicarpa* to 3m but less common. *X. johnsonii* showed 41 green scapes, 58 dry seeded scapes, 11 with foot prints and 5 scarred.

Site 4 (Fig. 14): Groundcover homogeneous throughout with *Smilax australis* rampant and up to 6 m. *L. ensifolia* common throughout, *H. actuigluma* sparse, *D. caerulea* common, *Pteridium esculentum*, *T. triandra*, *P. careya*, *Schizaea dichotoma* sparse, *Eustrephus latifolius*, *L. longifolia* common, *Clerodendrum longiflorum* var. *cunninghamii* common to 2m and often dense. *M. affine* forming clumps up to 2m high by 12m wide, *Alphatonia excelsa* sparse. Regenerating *A. flavescens* and *A. crassicarpa* to 3m common and forming 20% cover. Many dead acacias 8-10 m. *X. johnsonii* showed 80 green scapes, 131 dry seeded scapes, 51 with foot prints and 23 scarred

posed of *Planchonia careya* (O) and the ground layer (50% cover and heavily grazed) of probably *I. cylindrica* and other grasses.

2 & 3. ***Tinkle Creek** (18°39'20"S, 145°54' 55"E) and ***Lannercost Creek** (18° 38'20"S, 145°54'15"E). Dominant species in the upper canopy (22m with 30% cover), *E. platyphylla* (C), *E. clarksoniana* (C), *E. tessellaris* (C) and *E. drepanophylla* (C). Understorey (30% cover) composed of *P. careya* (C) and *Xylomelum scollianum*. Ground layer (50% cover and grazed) of *Cajanus reticulata* and *Heteropogon contortus*. Soil, coarse pale sand and rocks, TVT 16p. Foothills with a gentle slope (1:10).

4. **Ashton Creek** (18°37'41"S, 145°53'57"E). Glider not seen feeding. Dominant species in the upper canopy (24m with 35% cover), *E. tereticornis* (C), *E. platyphylla* (C), *E. clarksoniana* (C) and *E. tessellaris* (C). Understorey (20% cover) composed of *P. careya* (C), *A. crassicarpa* (O), *A. mangium* (O), *L. suaveolens* (O), *Albizia canescens* (U) and *Timonius timon* (U). Ground layer (50% cover and grazed) of *Hyptis capitata, I. cylindrica* and other grasses. Soil, brown sandy loam, TVT 20.

18° 37'26"S 145° 54'12"E. Gliders feeding in flowering *E. tereticornis*. Dominant species in the upper canopy (20m with 35% cover), *E. tereticornis* (C), *L. suaveolens* (A), *E. clarksoniana* (O), *E. tessellaris* (O), *A. crassicarpa* (O) and *Acacia mangium* (O). Understorey (<5% cover) of *P. careya* (O). Ground layer (30% cover and heavily grazed) of unidentified grasses. Soil, grey-brown sandy loam, TVT 20.

5. **Lannercost Creek** (18°37'13"S, 145°56' 44"E) (tongue of natural vegetation between exotic pine plantation and creek). Glider not seen feeding. Dominant species in the upper canopy (30m with 30% cover), *E. drepanophylla* (C), *E. dolichocarpa* (O), *L. suaveolens* (O), *E. tessellaris* (O), *E. platyphylla* (U) and *M. leucadendron* (C) on the creek. Understorey (10% cover) composed of *P. careya*, *Acacia crassicarpa*, *A. mangium* (creek), *Carallia brachiata* and *Dillenia alata*. Ground layer (60% cover and heavily grazed) of probably *I. cylindrica* and other un-

identified grasses. Soil, grey-brown loam, TVT 20.

6. **Elphinstone Creek** (18°29'42"S, 146°01' 26"E) (isolated *E. clarksoniana* on edge of cane field with remnant creek vegetation). Glider feeding on *E. clarksoniana* blossom. Dominant species in the upper canopy (20m with 30% cover), *L. suaveolens* (C), *E. platyphylla* (C) and *E. clarksoniana* (C). Understorey (<10% cover) composed of *P. careya* (C) and *A. crassicarpa* (C). Ground layer (80% cover) of *I. cylindrica* and *Themeda triandra*. Soil, grey-brown sandy loam, TVT 19.

7. **Porters Creek** (18°26'57"S, 146°07'35"E). Glider feeding on blossom of *E. pellita*. Gully with 20m buffer zone, bordered both sides by exotic pine plantation. Dominant species of the upper stratum (25m with 50% cover), *E. intermedia*, *E. pellita*. Understorey (30% cover) composed of *Casuarina torulosa* (C, almost forming canopy), *A. flavescens* (C), *A. crassicarpa* (O), *X. scottianum* (O), *A. mangium* (O), *P. careya* (C) and *Persoonia falcata* (O). Ground layer (60% cover) of *T. triandra*, *Pteridium esculentum*, *Lomandra longifolia* (C), *Mnesithea rottboellioides* (C). Soil, brown, sandy loam, TVT 16f (without *Syncarpia glomulifera* and *Banksia compar*).

18°26'47"S, 146°07'17"E. Glider not seen feeding. Dominant species of the upper stratum (25m with 50% cover), *E. clarksoniana* (C), *E. platyphylla* (C) and *Lophostemon suaveolens* (C). Understorey (20% cover) composed of *A. flavescens* (A) and *A. mangium* (O). Ground layer (60% cover) of *H. triticeus* (O), *T. triandra* (C) and *I. cylindrica* (A). Soil, grey-brown, sandy loam, TVT 19.

8. **Mullers Creek** (18°26'13"S, 146°07'15"E). Gliders not seen feeding, site logged and thinned out. Dominant species of the upper stratum (20m with 30% cover), *E. clarksoniana* (C), *E. platyphylla* (C) *L. suaveolens* (C), *E. tessellaris* (O), *Melaleuca dealbata* (O), and *Albizia canescens* (O). Understorey (<5% cover) composed of young *M. dealbata*. Ground layer (80% cover) of *T. triandra* (C) and *I. cylindrica* (A). Soil, grey-brown loam, TVT 19.

9. **Lumholtz National Park** (18°24'30"S, 145° 46'10"E (rainforest transition site by the Herbert R). Glider feeding on *Melicope elleryana* blossom. Dominant species in the upper canopy (22m with 50% cover), *E. tereticornis* (C), *M. elleryana* (O), *L. suaveolens* (C), *Aleurites moluccana* (O), Lauraceae sp. (O), and *E. torelliana*.

Understorey (40% cover) composed of *Mallotus philippinensis* (O), *Macaranga tanarius* (O), *Aphananthe philippinensis* (O), and *Lantana camara* (O). Ground layer (10% cover) of *Calamus caryotoides* and *Triumfetta rhomboidea*. Soil, brown sandy loam, TVT 19.

10. ***Cement Creek** (18°23'55"S, 146°05' 57"E). Site not surveyed.

11. **Kennedy Valley** (18°13'31"S, 145°55' 23"E). Site presumed. Closest woodland stand to location of specimen snared on barbed-wire fence. Dominant species of the upper stratum (22m with 40% cover), *E. tereticornis* (C), *E. pellita* (C), *E. drepanophylla* (C), *E. clarksoniana* (O), *Acacia mangium* (C) and *E. tessellaris* (U). Understorey (30% cover) composed of *A. flavescens* (C), *Pandanus* sp.(O), *Guioa acutifolia* (O), *Breynia cernua* (O) and *L. camara* (C). Ground layer (40% cover) of *T. triandra* (C) and *I. cylindrica* (A). Soil, brown loam, TVT 20.

12. **Baird Creek** (18°12'11"S, 145°58'17"E). Glider feeding on *E. tereticornis* blossom. Dominant species of the upper canopy (25m with 40% cover), *E. tereticornis* (C), *E. clarksoniana* (C),

FIG. 11. Vegetation surrounding Nest Site 1 (of Table 4), Barretts Lagoon. Den tree is arrowed.

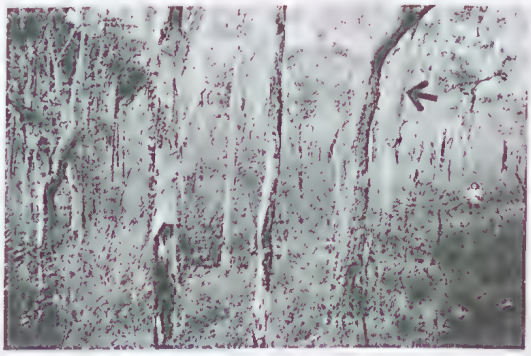


FIG 12. Vegetation surrounding Nest Site 2 (of Table 4), Barretts Lagoon. Den tree is arrowed.

A. mangium (C), *E. tessellaris* (O), *Melaleuca dealbata* (O) and *Melicope elleryana* (O). Understorey (50% cover) composed of *Alphitonia excelsa* (C), *Glochidion ?lobocarpum* (C), *B. cernua* (C), *Acacia flavescens* (C), *Polyscias elegans* (C) and *Planchonia careya* (O). Ground layer (<5% cover) of *Alpinia caerulea* (U) and *I. cylindrica* (U). Soil, grey-brown loam, TVT 19.

13. **Edmund Kennedy National Park** (18° 12'04"S, 145°59'14"E). Glider not seen, call only recorded. Dominant species of the upper canopy (25m with 45% cover), *E. tereticornis* (C), *Acacia mangium* (C), *Lophostemon suaveolens* (C), *E. tessellaris* (U), *Melaleuca dealbata* (O) and *E. intermedia* (O). Understorey (30% cover) composed of *Alphitonia excelsa* (O), *G. ?lobocarpum* (C), *A. crassicarpa* (C), *P. elegans* (C), *D. alata* (C) and *Pandanus* sp.(O). Ground layer (30% cover) of *I. cylindrica* (A), *Pteridium esculentum* (O), *T. triandra* (O), *Cycas media* (U), *Heteropogon ?triticeus*, with *Cymbidium madidum*, *Platycorys hillii* and *Smilax australis* (C). Soil, grey sand, TVT 19.

18°08'43"S, 145°57'50"E. Although this glider was recorded east of (and hence inside) the Edmund Kennedy National Park fence line, the site does not actually occur within the National Park. The fence does not accurately reflect the gazetted east-west boundary. Glider not seen, call only recorded. Dominant species of the upper canopy (20m with 35% cover), *E. pellita* (A), *E. intermedia* (C), *L. suaveolens* (O) and *Deplanchea tetraphylla* (U). Understorey (30% cover) composed of *A. flavescens* (C), *A. crassicarpa* (C) and *Dillenia alata* (O). Ground layer (40% cover) of *Melastoma affine* (C), *Gahnia sieberiana* (O) and *Scleria ciliaris* (A). Soil, grey sandy loam, TVT 19.

Glider moved from this site into adjacent tea-tree swamp where the dominant species of the upper canopy (15m with 50% cover) was *Melaleuca quinquenervia.* Ground layer (95% cover) of *Melastoma affine* (C), *G. sieberiana* (O), *A. pubirhachis* (C), *Rhynchospora* sp. (C), *Schoenus ?melanocephalus* (C), *Lycopodium cernuum* (O), *Leptocarpus ramosus* (A), *Eriocaulon* sp. (A), *Ischmaeum* sp. (C) with *Drosera spathulata*, *Myrmecodia beccarii* and *Dischidia nummularia*. Soil, grey sandy loam, TVT 15a.

14. **Dalachy Creek** (18°09'26"S, 145°57' 26"E). Glider feeding on flowering *E.clarksoniana* in cleared paddock. Vegetation proforma of closest adjacent site (creek community). Dominant species of the upper canopy (20m with 80% cover), *A.mangium* (C), *A. aulacocarpa* (C), *Lophostemon suaveolens* (C), *Tristaniopsis exiliflora* (C), *Eucalyptus intermedia* (U). Understorey (30% cover) composed of *Alstonia muelleri*, *Polyscias elegans* and *P. australiana.* Ground layer (<1% cover) of *Piper novaehollandiae*, *Lygerdum* sp., *Tetracera nordtiana* and *Lomandra hystrix.* Soil, brown loam, TVT 24 (cleared near TVT 1a).

18°08'51"S, 145°57'40"E. Glider feeding on flowering *E. pellita.* Dominant species of the upper canopy (20m with 30% cover), *E. pellita* (C). Understorey (40% cover) composed of *Lophostemon suaveolens* (C), *Acacia flavescens* (C), *A. crassicarpa* (C), *Dillenia alata* (O), *Pandanus* sp. (C) and *Melaleuca quinquenervia* (C). Ground layer (30% cover) of *Scleria ciliaris* (A) and *Blechnum indicum* with *Dendrobium smilliae* and *Drynaria rigidula.* Soil, grey-brown sandy loam, TVT 19.

15. **Murray Upper** (18°08'38"S, 145°47' 54"E). Rainforest transition site, gully with 20m buffer zone, bordered both sides by pine plantations, glider not recorded feeding. Dominant species in the upper canopy (20m with 40% cover), *E. pellita* (C), *E. clarksoniana* (C), *A. mangium* (C), *E. tessellaris* (C) and *L. suaveolens* (C). Understorey (70% cover) composed of *A. flavescens* (C), *Guioa acutifolia* (O), *Scolopia braunii* (C), *Timonius timon* (C), *Dillenia alata* (C), *Rubus moluccanus* (C) and *Polyscias australiana* (C). Ground layer (<2% cover) of *Smilax australis* (C), *Hysperpalaurina* sp. (C) and *Lomandra longifolia.* Soil, brown sand, TVT 19 .

16. **Bilyana** (18°07'S, 145°56'E). Mounted specimen in private collection of T. Marsilio for which the only collection details (from card attached to specimen) are as follows: 'Fly Squerrel was killid in falling tree in front of Joe Ottone while Alec was clearing line for El. Power. at Bilianna on Bluff Road. 15 ?years ago'. TVT 24 with remnants of 19.

17. ***Murray Upper** (18°06'30"S, 145°49' 40"E). Dominant species of the upper canopy (25m with 40%cover), *E. tereticornis* (C), *A. mangium* (C), *E. tessellaris* (O), *M. dealbata* (O), *E. clarksoniana* (C) and *Melicope elleryana* (O). Understorey (50% cover) composed of *Alphitonia excelsa* (C), *Glochidion ?lobocarpum* (C), *A. flavescens* (C), *Polyscias elegans* (C), *Breynia cernua* (C) and *Planchonia careya.* Ground layer (<5% cover) of *I. cylindrica* (U) and *Alpinia caerulea* (U). Soil, grey-brown sand, TVT 19.

18. **Yingalinda Beach** (18°03'18"S, 146°01' 37"E). Glider recorded in *E. intermedia.* Dominant species in the upper canopy (35m with 35%

cover), *E. intermedia* (C) and *L. suaveolens* (C). Understorey (40% cover) composed of *A. flavescens* (A), *A. crassicarpa* (A), *Polyscias elegans* (O), *Alstonia muelleri* (O), *Canarium australiana* (O), *Deplanchea tetraphylla* (O) and *Planchonia careya*. Ground layer (20% cover) of *Scleria sphaolata* (C), *Pteridium esculentum* (C), *I. cylindrica* (C) and *Xanthorrhoea johnsonii* (O) with *Smilax australis*, *Eria fitzalanii*, *Dendrobium smilliae* and *Cymbidium madidum*. Soil, grey sand, TVT 17.

19. **Barretts Lagoon**. (i) South western bank (18° 02'31"S, 145° 58'36"E). Gliders recorded feeding on flowering *Eucalyptus tessellaris*. Site cleared Feb 1990. Prior to that the dominant species in the upper canopy (35 m) were *E. pellita*, *E. intermedia*, *Acacia mangium*, *E. tessellaris*, *E. tereticornis* and *L. suaveolens*. Understorey (9m and 80% cover) composed of regenerating *A. flavescens*, *Planchonia careya*, *A. crassicarpa*, *Melastoma affine*. Ground layer (20% cover and grazed) of *I. cylindrica* and *Themeda triandra*, *S. australis* and *Lomandra longifolia*. Soil, grey sand, TVT 24 with remnants of 17.

(ii) North eastern bank (18°02'22-23"S, 145°58'52"E). Gliders recorded feeding and heard grunting in flowering *E. tereticornis*. Remnant vegetation along immediate edge of Barretts Lagoon. Isolated specimens (to 30m) of *A. mangium*, *E. tessellaris* , *L. suaveolens*, *M. leucadendron* and *M. dealbata*. TVT 24.

(iii) 'Rice Fields' (18°01'26"S, 145°58'46"E). Gliders feeding in *E. pellita*, *E. intermedia*, *L. suaveolens*, *X. johnsonii*. See detailed vegetation analysis 'Nest site 3', Table 4. TVT 17.

(iv) East (18°01'33"S, 145°59'34"E). Gliders feeding in *X. johnsonii* and *M. dealbata*. Dominant species in the upper canopy (20m with 50% cover), *E. pellita* (C), *E. intermedia* (C), *L. suaveolens* (C), *A. crassicarpa* (C), *M. dealbata* (O), *Deplanchea tetraphylla* (U). Understorey (30% cover) composed of *A. flavescens* (C), *M. viridiflora* (C), *Banksia integrifolia* var. *aquilina* (U), *Casuarina littoralis* (C) and *Pandanus* sp. Ground layer (40% cover) of *T. triandra* (C), *L. longifolia* (C), *Lindsaea ensifolia* (A), *Leptocarpus ramosus* (A) and *X. johnsonii* (A). In wetter gullies at base of swales, dominant canopy species (18-20m with 50% cover) changed to *E. pellita* (A), *Lophostemon suaveolens* (A) and *A. mangium* with an understorey (15% cover) of *A. flavescens* (O), *A. crassicarpa* (O), *Pandanus* sp.(O) and *Dillenia alata*. Ground layer (30% cover) of *Gonocarpus ?acanthocarpus* (C), *Lindsaea ensifolia* (C), *Dicranthopteris linearis* (O), *Melastoma affine* (C), *Eriocaulon* sp., *Scleria laevis* (C), *Ishmaeum australe* (A), *Flagellaria indica* (O) with *Eria fitzalanii* and *Dendrobium smilliae*. Soil, dark drown sandy loam, TVT 17.

20. **Hull River** (17°58'29"S, 146°02'02"E). Glider feeding in *E. intermedia*. Dominant species of the upper stratum (30m with 40% cover), *Eucalyptus intermedia* (C), *E. pellita* (A), *A. mangium* (C), *Lophostemon suaveolens* (O) and *Deplanchea tetraphylla* (O). Understorey (70% cover) composed of *Davidsonia pruriens* (C), *Polyscias australiana* (C), *A. muelleri* (C), *Dillenia alata* (O), *Wilkiea nuegeliana* (C), *Rhodomyrtus* sp., *Pandanus* sp., *Syzygium wilsonii*, *Lepidozamia hopei*, and *A. flavescens* (A). Ground layer (<10% cover) of *Calamus caryotoides*, *C. moti*, *Smilax australis*, *F. indica*, *Lygopodium* sp., with *Eria fitzalanii*, *Dendrobium smilliae*, *Cymbidium madidum* and *Platycorys hillii*. Soil, brown sand to sandy loam, TVT 17 adjacent to TVT 15a.

Spotlighting

Spotlighting surveys for *P. gracilis* were conducted at a number of sites (Table 3). The species was recorded at 16 of the 36 localities and represented a total of 1334 manhours of observation. In habitats supporting *P. gracilis*, the most commonly observed arboreal marsupial assemblage comprised *P. gracilis*, *Dactylopsila trivirgata*, *P. breviceps* and *Acrobates pygmaeus*. The presence of this group of exudivores and insectivores and the obvious absence of such foliovores as *Trichosurus vulpecula*, *Pseudocheirus peregrinus*, *Petauroides volans* and *Phascolarctos cinereus* may have been a reflection of possible nutritional deficiency in vegetation of the coastal alluvium, however this was not addressed in the study.

Trichosurus vulpecula was extremely rare in habitat considered optimal for *P. gracilis*. Only 1 specimen of the brushtail was recorded near such habitat (Dalachy Creek) and at that site *T. vulpecula* was recorded from a tree isolated in improved (fertilised) pasture. Where *T. vulpecula* occured commonly with *P. gracilis* (e.g. Wharps Holding) the habitat was considered marginal or poor for the glider.

Bioclim Prediction

A climate profile (Table 5) was generated by the BIOCLIM prediction system (see Nix & Switzer, 1991) after completion of field surveys. Using core predictions [geographic points matching all 28 climatic values (7 for radiation, 7 for

temperature, 7 for precipitation and 7 for moisture index) between the 5% and 95% values (the 90 percentile range) in the climate profile] the presence of *P. gracilis* was predicted beyond that area encompassed by the field results presented in Table 1 only on the north western tip of Hinchinbrook Is. (Fig. 15). Soils of the north western tip developed in situ largely from massive rhyolitic to dacitic volcanics and to a much lesser extent riebeckite granite near Scraggy Point. The north western lowland woodland communities there do not reflect a mirror image of the woodlands of the Coastal Floodplains and Piedmont Slopes (TVT 19) across the Hinchinbrook Channel on the mainland. Many potential sites (TVT 13e, 15b) appeared to be losing their identity under the encroachment of rainforest species, and drier forest types tended to be dominated by *Eucalyptus clohesiana* which grew from near sea level to well above the 100m contour. To date *P. gracilis* has not been recorded from *E. clohesiana*. In Sept 1992 two nights were spent surveying in woodland slopes supporting *E. intermedia*, *E. clohesiana*, *E. tessellaris*, *E. acmenoides*, *Melaleuca leucodendron*, *Pandanus* sp. and *Xanthorrhoea johnsonii* (Table 3) without success. Hinchinbrook Is. should be resurveyed for *P. gracilis*.

Using marginal predictions (all 28 climate values falling within the total range in the climate profile) *P. gracilis* was again only predicted to occur inside the core area plotted for the north west tip of Hinchinbrook Is.

Trapping

A total of 721 trapnights resulted in the capture of one *P. breviceps* from degraded habitat being cleared at Barretts Lagoon (16 Feb 1991). No *P. gracilis* were collected by this method in spite of the trapping program being conducted under the on-site advice of field researchers skilled at capturing other petaurids such as *P. breviceps*, *P. australis* and *P. norfolcensis*. The degree of difficulty in trapping *P. gracilis* by traditional methods greatly impinges on the understanding of its social organisation which is fundamental to the process of estimating its population density.

Artificial Hollows

Two sub-adult female *P.gracilis* (ear tagged T4027, T4028) were caught together in 'nestbox' No. 8 on 10 May 1991. No other *P. gracilis* were trapped by this method but other individuals were known to use the tubes e.g. radio-tagged adult male T4030 was recorded once (7Aug 1991) in 'nestbox' 12, and an unmarked adult male (possibly T4030) escaped from 'nestbox' 27 before the entrance could be reached and plugged (4 Aug 1991). Subadult female T4028 used 'nestbox' 12 and 13 on 5 days during the period 11-19 May 1991. Tubes were more frequently inhabited by Brown Tree-snakes (*Boiga irregularis*), Green Tree Ants *(Oecophylla smaragdina)* and less frequently by Sugar Gliders *(P.breviceps)* (adult male and female, 'nestbox' 14, 25 May 1992; group in 'nestbox' 7 (east), 8 Oct 1992).

Home Range Determination

Shortcomings associated with this part of the study are referred to under 'Methods'. Results of home range analysis and plots of dens appear in Figs 16-19. The 95% isopleth of the harmonic mean distance minimum gave a value of 23.01ha for adult female T4026 (110 fixes), 9.04ha for sub-adult female T4027 (36 fixes) and 13.86ha for sub-adult female T4028 (36 fixes). These results should be taken as preliminary and minimal as the plots indicate that the curves have not quite asymptoted (see Quin et al., 1992; Goldingay, 1992). Areas estimated using the miminum convex polygon (MCP) were 18.65, 16.48 and 10.96ha respectively. Overlap is shown in Fig. 19. Possible underestimation of home range size could be partly or wholly offset by patches of treeless swale included in the estimates. Subadults T4027 and T4028 may have been dispersing offspring of T4026. Insufficient fixes were taken of adult male T4030 (who dislodged his transmitter after 3 nights) or female T4031 (for which den fixes only were taken) to allow estimation of home ranges. However, male T4030 was known to have moved between the home range of adult female T4026 and one of the dens of adult female T4031 (see 'Reproduction' and Fig. 19). Serial den use (Kehl & Boorsboom, 1984) was noted between adult female T4026 and sub-adult female T4028, adult male T4030 and sub-adult female T4028 . Conjoint den use was noted between adult male T4030 and adult female T4026, adult male T4030 and adult female T4031, and between the two sub-adult females T4027 and T4028.

Reproduction

Petaurus gracilis appears to give birth in the spring, although this pattern is complicated by the record of hairless young in the pouch of a female collected in mid-February and an observed September copulation involving a female known to be carrying two hairless pouch young.

Two adult females captured 5 and 9 Aug 1991

FIG. 13. Vegetation surrounding Nest Site 3 (of Table 4), Barretts Lagoon. Den tree is arrowed.

(T4026 and T4031 respectively) each carried two hairless pouch young. Young measured approx 35mm crown to cloaca. Females resisted attempts to examine pouch young by contracting muscles surrounding the pouch opening. By 26 Nov 1991 young of T4026 [T4032 (M) and T4033 (F)] weighed 65g and 69g (respectively) (see Table 2 and Fig. 20) and the pouch of T4026 was noted to be divided longitudinal into two halves by a thin septum (see Calaby, 1966 for description in *P. australis*). The right pouch side was thinly covered with long ginger-brown hairs and the left contained two elongated nipples, each 6mm long. Adult female T4031 was not recaptured. The pouch of adult female JM7290 collected 14 Feb 1973 contained two hairless young. The pouch of female JM8549 (which died ensnared on a barbed wire fence Oct 1990) contained one newly furred young JM8550 (43g). The right posterior corner of the pouch contained well developed mammary tissue, anterior to which (close to the body) was a covering of long ginger hair. The single nipple measured 11mm.

The following copulatory behaviour was noted between female T4026 and male T4030 (both captured in *Lophostemon suaveolens* den, nest site 3 of Table 4, Sept 5 1991) at a time when female T4026 was carrying 2 hairless pouch young. Observations on 7 Sept 1991 commenced at 1900hrs with female motionless in *L. suaveolens* close to den. At 2030hrs, male T4030 appeared in tree 7 metres away from the tree in which the female was sitting. Both remained motionless until 2100hrs. The male then produced a soft but hoarse call resembling 'chew-chew-chew-chew' at which the female made immediate efforts to join him (but was interrupted by noise from observers on the ground). At 2226hrs the male glided to the female's tree. The female appeared to sniff and lick the male's rump (probably applying male scent as observed in *P. australis* by Henry & Craig, 1984; Russell, 1984) and followed him up the trunk to sit together in the canopy. The female then glided to a nearby large *E. pellita*, was followed by the male and the two remained motionless, 'curled up' around one another in the canopy until 0040hrs. The female then leapt to a nearby tree and was followed closely by the male. From 0057hrs to 0155hrs the two remained motionless in a 'ball' whereupon the male lunged at the female and the two copulated until 0217hrs. During copulation male and female adopted a vertical, head-down position on the trunk with the female's head pushed against an ant plant (*Myrmecodia beccarii*). The male thrust intermittently, grasping the female's dorsum in a position not unlike that adopted by young back-riding gliders newly emerged from the pouch. A neck bite was maintained by the male until the two separated, whereupon the male licked and groomed his penis. The female leapt to a nearby *E. pellita*, was followed by the male and the two sat closely and motionless until 0400hrs whereupon the female made bursts of 'glide-and-freeze' (thought not to be induced by the presence of observers) toward a den which was some way off and reached by 0545hrs. The male had lost interest in the female by 0400hrs and moved elsewhere. The male did not share the den occupied by female adult T4026, but shared an *E. intermedia* den occupied by another adult female, T4031 (with pouch young). This den could be reached over a minimum distance of approx 1.5km from where T4026 and T4030 separated.

The following night (8 Aug 1991) observation commenced with female T4026 at 1830hrs. At

TABLE 5. BIOCLIM climate profile for *Petaurus gracilis* in tropical north Queensland based on all Queensland Museum records and observations. Temperature (°C); precipitation (mm); radiation (MJ/m^2/day); moisture index [0 (moisture totally limiting to growth) -1 (moisture non-limiting to growth)]. Seasonality (coefficient of variance for 12 monthly values as %).

CLIMATE PARAMETER	Min	Percentile		Max
		5	95	
Annual mean temperature	23.78	23.80	23.94	23.95
Coldest month mean minimum temperature	12.73	12.80	14.09	14.09
Warmest month mean minimum temperature	31.77	31.81	32.69	32.74
Annual range (mean max-mean min temperature)	17.67	17.71	19.89	20.01
Wettest quarter mean temperature	26.65	26.68	26.96	26.97
Driest quarter mean temperature	20.00	20.12	22.22	22.30
Seasonality (coefficient of variance)	11.87	11.90	13.04	13.08
Annual mean rainfall	1528.76	1572.11	3176.25	3262.96
Wettest month mean rainfall	345.24	352.32	628.63	628.63
Driest month mean rainfall	14.48	20.60	69.54	76.66
Annual range (wettest month-driest month)	323.59	331.48	557.40	560.36
Wettest quarter mean rainfall	1012.90	1033.28	1828.06	1828.06
Driest quarter mean rainfall	54.84	60.89	230.45	236.50
Seasonality (coefficient of variance)	80.63	83.05	104.24	104.85
Annual mean daily solar radiation	18.81	18.90	19.69	19.72
Highest monthly mean daily solar radiation	24.92	24.97	25.41	25.42
Lowest monthly mean daily solar radiation	13.46	13.57	14.52	14.56
Annual range of monthly mean daily solar radiation	10.66	10.74	11.14	11.47
Wettest quarter mean daily solar radiation	19.76	19.76	20.10	20.10
Driest quarter mean daily solar radiation	16.06	16.27	20.07	20.21
Seasonality (coefficient of variance)	17.84	18.12	19.79	20.63
Annual mean moisture index	0.63	0.64	0.92	0.92
Wettest month mean moisture index	1.00	1.00	1.00	1.00
Driest month mean moisture index	0.15	0.16	0.54	0.59
Annual range (wettest-driest month)	0.41	0.46	0.85	0.85
Wettest quarter mean moisture index	0.98	0.98	1.00	1.00
Driest quarter mean moisture index	0.25	0.31	0.86	0.87
Seasonality (coefficient of variance)	15.97	17.33	55.37	56.72

1930hrs the female began moving between trees with apparent resolve only to sit 'frozen' for extended periods then move off in the same manner. Male T4030 appeared in a nearby tree at 2318hrs. The female made soft 'chee-chee-chee-chee' calls which brought the male into her tree. The two sat closely until 0200hrs (when observations were abandoned). The pair did not share a daytime den.

The next night (9 Aug 1991) the same pair were noted consorting (only) from 2305-0100hrs. Observations continued to 15 Aug 1991 but the pair were not seen to consort again.

DENNING (see Table 4)

A total of 19 dens were recorded at Barretts Lagoon (see Figs 16-19). These varied from a dead stag of undetermined species (13m) to living examples of *E. intermedia* (8), *L. suaveolens* (2), *M. quinquenervia* (2), and *E. pellita* (6) up to 27m in height (Figs 11-14). In tall trees it was usually impossible to determine either the den entrance or the den position inside the trunk. In two cases (sites 1 and 3, Table 4), both were known. At site 1 (Figs 11 and 21) the den was made in a 7m living *E. intermedia*. The 50mm entrance hole was 5.8m above ground, the nest cavity approx. 200mm dia. and the nest of dried leaves approx 3m below the entrance. At site 3 (Figs 13 and 22) The den was made in a 10m living *L. suaveolens*. The 45mm entrance hole was 3.8m above ground, the nest

FIG. 14. Vegetation surrounding Nest Site 4 (of Table 4), Barretts Lagoon. Den tree is arrowed.

cavity approx. 250mm diameter and the nest of dried leaves approx. 50cm below the entrance.

There was no apparent shortage of hollow limbs and termite-ravaged trunks in the woodland habitat occupied by *P. gracilis* and while individual gliders showed preference for certain dens they regularly moved nests and used a variety of widely separated dens through their home range (Figs 16-19), e.g. in the period 10-20 May 1991, adult female T4026 used the 'favoured' nest (nest site 3 of Table 4) on 4 of those days and 7 different dens on the seven remaining days. This female was recorded using a total of 10 different dens.

In addition, gliders familiarised themselves with the mature trees of their home range and spent considerable time exploring hollows and holes in trees other than those known to contain dens. In one case, on consecutive nights, female T4026 descended to investigate a large, long, burnt-out log lying on the forest floor. On both nights the end of the log was entered at ground level and the glider crawled inside to finally peer out a ground-level pophole for approx 30min before returning to the trees. (On investigation, the inside of the log was found to contain crumbled charcoal, soil and remains of goanna skin, some Echidna quills and some patches of pungently smelling possum fur (? *Dactylopsila trivirgata*).

Nests in dens consisted of a thick mat of eucalypt leaves. Animals were not observed collecting or carrying these.

Vocalisation

Petaurus gracilis was quiet and difficult to locate by calls. The most commonly heard call was a deep, nasal, coarse grunt 'na-when, na-when'. It was not always possible to determine the sex of animals making this call, but those that were sexed were males. The call was sometimes made in response to the play-back defense gurgle ('urga-urga-urga', common to other Petaurids) of another individual (see Van Dyck, 1992b). It was also made in response to a human imitation of the 'na-when' call, and imitation was used to survey potential glider sites. One male was heard monotonously repeating this call. This individual was located 3m above ground, pressed head down against the trunk of a *Pandanus citraceus* and in its manner resembled a calling *P. breviceps*. This call was often shortened to a single nasal grunt 'hoy', and often appended by a low 'urga' or two. One sub-adult female once made the simple grunt 'arrgh' on detecting an adult female in a tree nearby. Animals unsure of their security (when exploring unfamiliar territory or when being handled) uttered a soft 'tock-tock'. Calls associated with consorting have been described under 'Reproduction'. Nestling young reunited with their mother after brief separation made a soft 'tzzz-tzzz' call on contact with the female.

Diet

The diet was assessed by directly observing gliders feeding or by analysis of faeces from captured individuals. The feeding observations described below are summarised in Table 6. See Van Dyck (1992b) for further discussion.

Nectar and pollen: Gliders were observed licking nectar (and presumably pollen) from the flowers of a range of trees and shrub species (Table 6). Five faecal pellets were collected during 4 months in 1991 and analysed for food items (Table 7). The pollen assemblage in February was entirely of Myrtaceae pollen, most of which was

FIG. 15. Core and marginal predictions of *P. gracilis* distribution generated by the BIOCLIM prediction system. (Dotted line shows actual profile of coast).

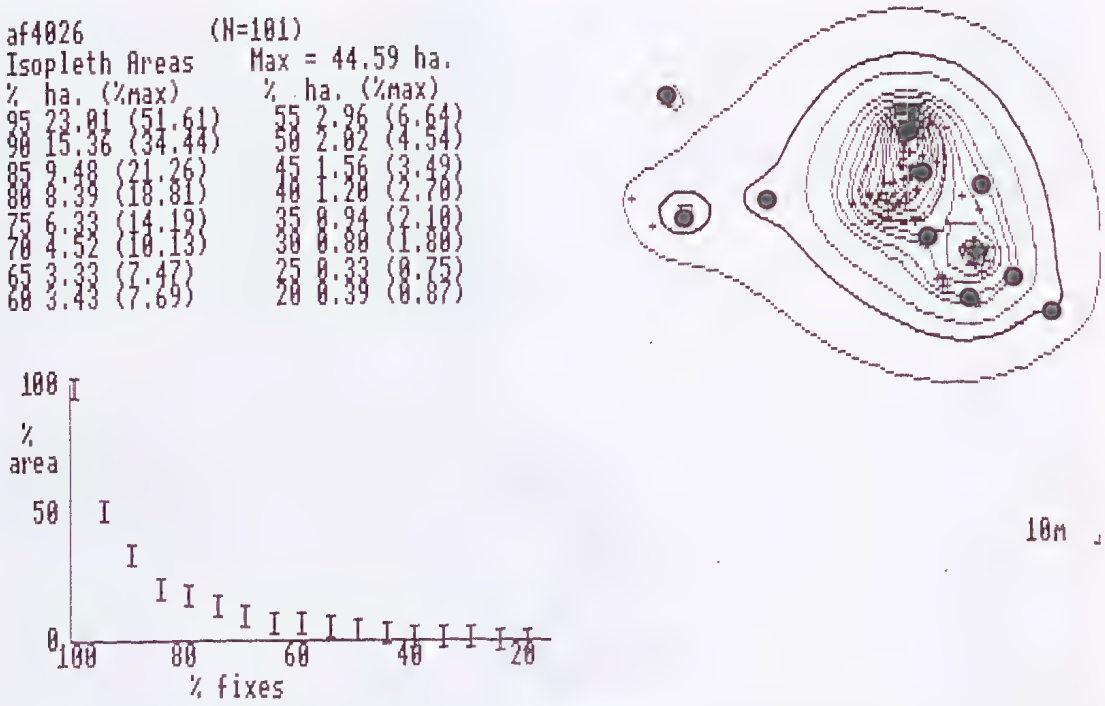


FIG. 16. Harmonic Mean Measure of home range and analysis for adult female T4026. Hard line is drawn over the 95% isopleth. Dots indicate dens used.

comparable to that of *Eucalyptus*. In May, plant material dominated the sample, but pollen was represented in low proportions; also represented were rhomboids of silica. The pollen assemblage contained approximately equal proportions of pollen of *Banksia* and *Xanthorrhoea*. *Banksia integrifolia aquilina*, the only species of banksia recorded at Barretts Lagoon occured very rarely at the study site.

One female glider was noted eating flower tassels of *Acacia crassicarpa* (each approx. 40mm long: 1 on 12 May 1991, 6-8 on 16 May 1991). Since this wattle produces no discernable nectar it was concluded that such ingestion constituted deliberate pollen feeding.

Xanthorrhoea johnsonii:Two radio-tagged female gliders (T4027, T4028) were observed over extended periods feeding on *X. johnsonii* during May 1991 when flowering was heavy (Table 6). Evidence of scape visitation ('scape' is used for the woody spear-like stalk of the *Xanthorrhoea* fruiting body) at other sites through footprinted scapes (see Fig. 23 and Van Dyck, 1992b) and scape damage, suggested that many other *P.gracilis* visited *X. johnsonii* (e.g. % green scapes footprinted at Nest Site (NS) 1 (see Table 4): 22%; NS2: 25%; NS3: 26%; NS4: 63%). The gliders' process of appraisal of the condition of scapes of *X. johnsonii* was conducted mostly at heights of less than 3m above the ground. Scapes were reached by leaps between thin saplings, small shrubs, dead sticks or other scapes. After landing on a scape, a glider would face downward, descend to within 30cm of the base, then turn and climb quickly up the spear. To reach more isolated scapes gliders crossed open ground in a series of rabbit-like hops through long grass. Fresh spikes ('spike' is used for the flowering head of the *Xanthorrhoea* fruiting body) were glided onto directly, but dried, seeded spikes were not, and although scapes of the previous season were climbed and investigated, the appraisal was abandoned usually within 30-60cm of the spike.

Young scapes with unformed spikes were chewed at the spike base and also at the scape base (Fig. 24) among the leaf insertions, and any amber-coloured mucilagenous exudate from earlier gougings licked off and eaten. *Xanthorrhoea* evaluation by *P. gracilis* occurred in frenetic bouts which ran for as long as 2.5hrs and covered linear distances of up to 800m. Suitable flowering heads were licked thoroughly for nectar (Fig. 25).

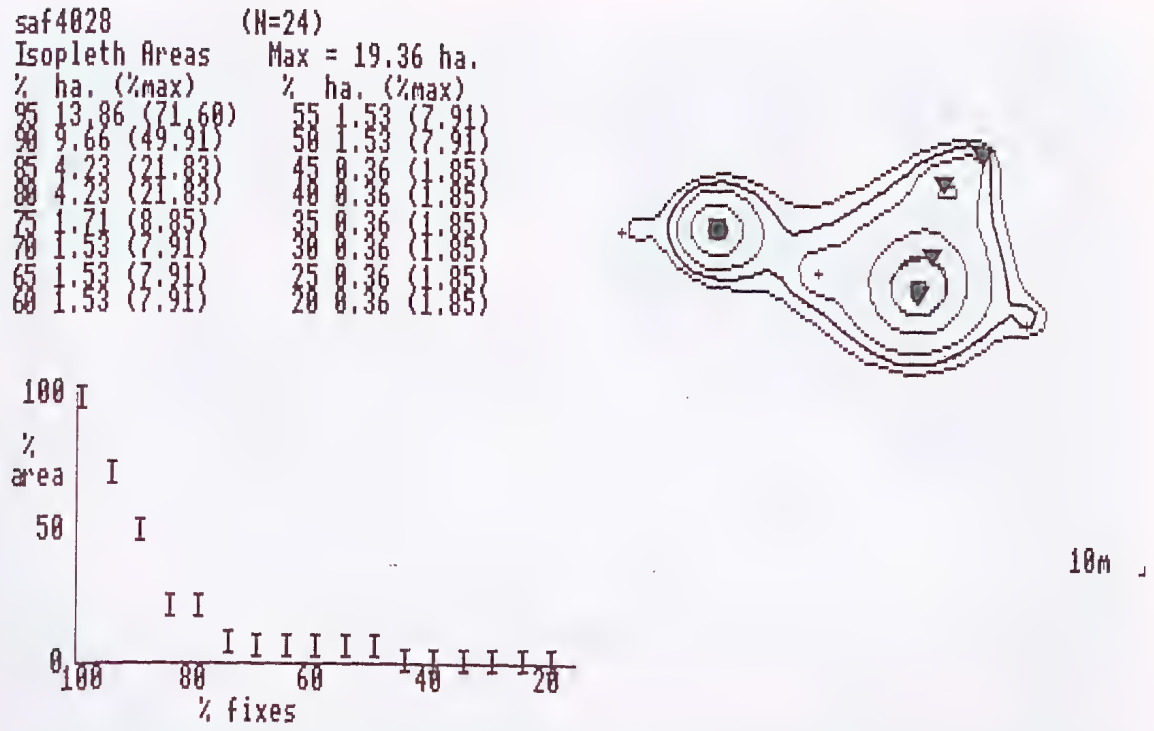


FIG. 17. Harmonic Mean Measure of home range and analysis for sub-adult female T4028. Hard line is drawn over the 95% isopleth. Dot indicates den used serially with adult female T4026. Triangles indicate other dens used.

One instance of eating unopened flowers was noted.

By August 1991 most *X. johnsonii* flowers had seeded (e.g. NS 1: 80%; NS 2: 50%; NS 3: 58%; NS 4: 62%) and experimental cuts which I made (5 Aug 1991) on immature scapes had produced no exudate up to 5 days after cutting. Although nectar-producing flowers occurred in the study area and pollen was abundant in one of two faecal samples taken (6, 9 Aug) (Table 7), none of the three gliders tracked during this period were recorded feeding on them. Hall (1956) demonstrated significant changes in spike component analysis from preflowering through to flowering. These included drops in protein (11.1% to 6.8%), carbohydrate (63.7% to 45.9%), fat (2.2% to 1.2%), phosphate (0.47% to 0.31%) and an increase in fibre (19.0% to 42.7%) as the spike matured.

Preliminary analysis results of dried gum exudate scraped from *X. johnsonii* scapes in Aug 1991 were as follows: moisture= 25.6%, protein (N×6.25)=2.5%. Infra-red spectroscopy showed that the substance was a complex mixture consisting of polymerised and/or unpolymerised higher alcohols and acids. Some carbohydrates in free or bound form were probably also present, but no simple sugars were detected (N. Douglas, pers. comm.). No analysis was made of May *Xanthorrhoea* exudate.

Eucalyptus intermedia and E. pellita sap and/or kino: Gliders were often observed feeding at wound sites on *E. intermedia* (Table 6). Here they would pick crusts of dried exudate and lick the surface from which the crust had been taken. The wound was often accompanied by fresh red dribblings of kino which may have been ingested also.

One female glider (T4026) was observed licking and stripping fresh and old longitudinal incisions in the canopy branchlets of *E. intermedia* and *E. pellita* (Table 6). From the *E. intermedia* canopy the process was difficult to observe clearly, but large lumps of hard exudate falling from the glider's mouth were collected on the ground. The process was observed between 2050hrs 11 Aug 1991 and 0327hrs 12 Aug 1991 and involved alternating bouts of licking-biting and motionless rest with mouth away from the wound and eyes often closed (10min feeding, 1hr

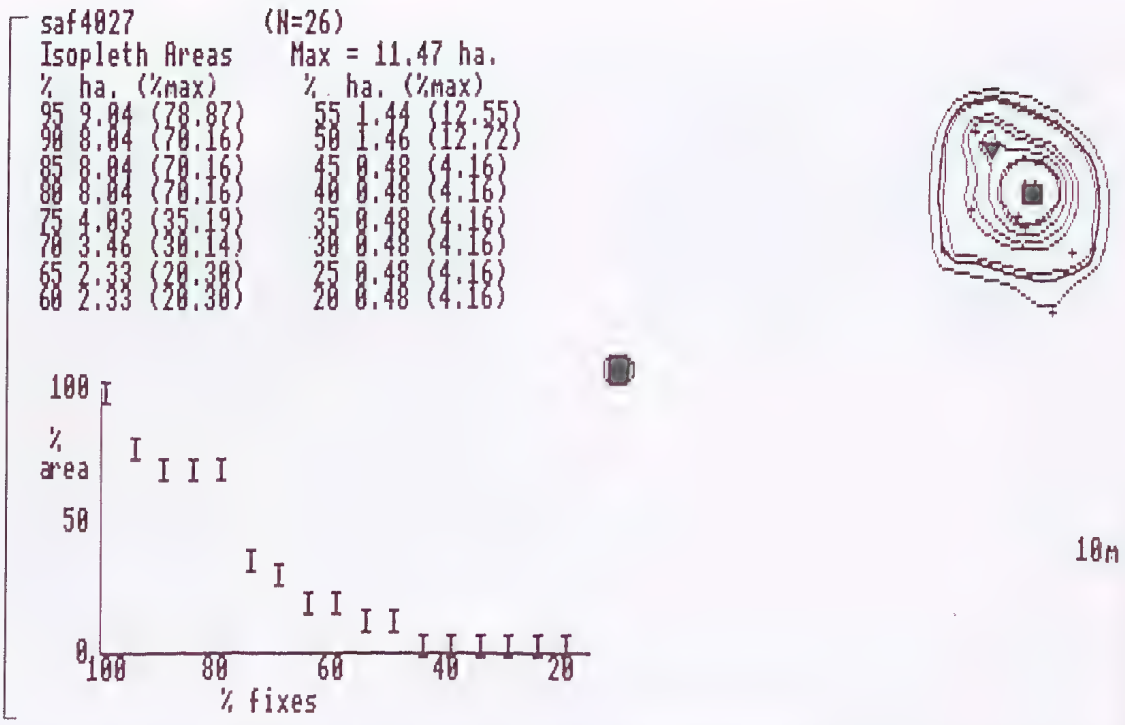


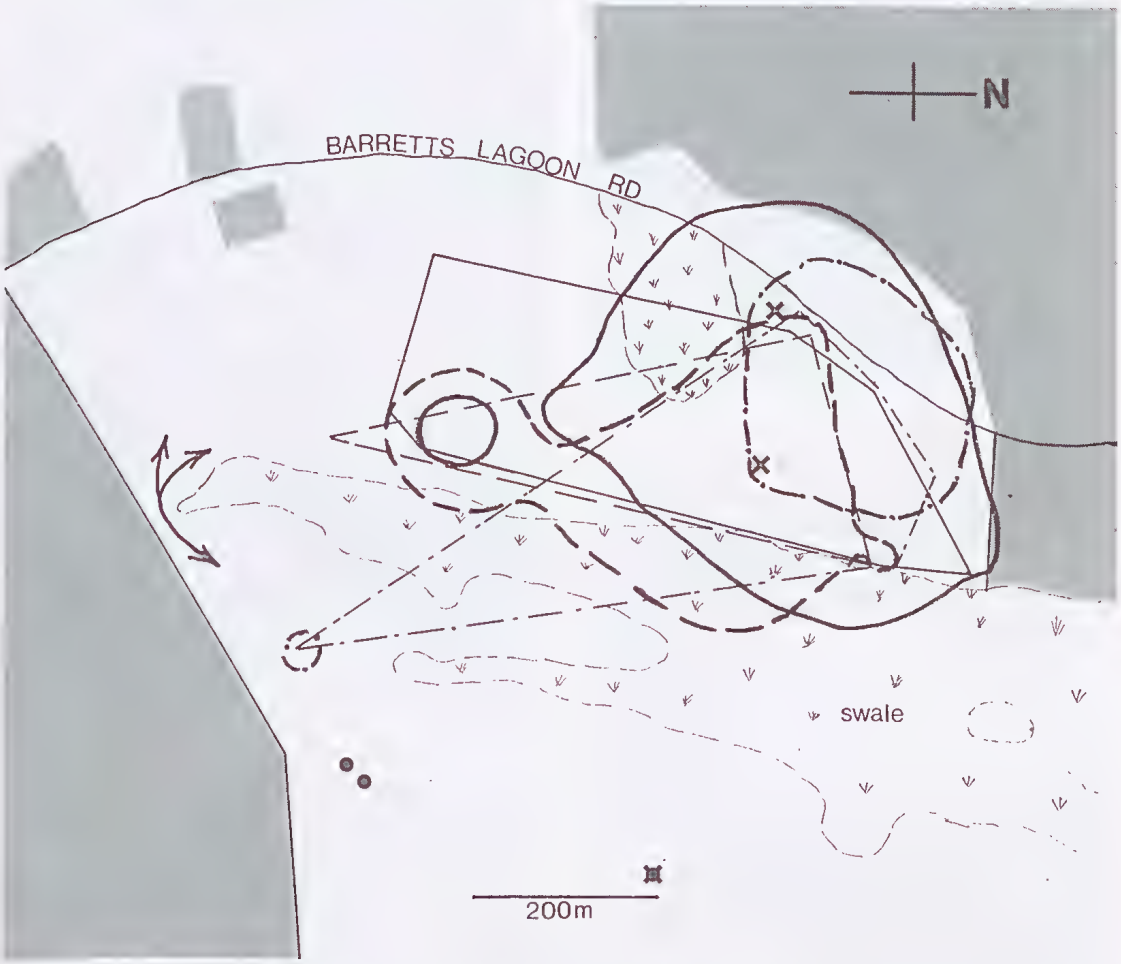
FIG. 18. Harmonic Mean Measure of home range and analysis for sub-adult female T4027. Hard line is drawn over the 95% isopleth. Triangle indicates den used conjointly with sub-adult female T4028. Squares indicate other dens used.

25min resting, 6min feeding, 28min resting, 7min feeding, 16min rest, 9min feeding, 5min rest. Total time feeding in *E. intermedia* 57min; total time resting 2hrs 27min. For *E. pellita* total time feeding 29min; resting 36min). Branchlets retrieved the following day from the feeding sites (approx. 17m high in the *E.intermedia* and approx. 8m in the *E. pellita*) showed many incisions of varying size and state of repair on thin branches that ranged from 4.7mm to 14mm in diameter (Fig. 26). For the *E. intermedia* sample (diameter 4.7- 12.9mm), incised cut lengths varied from 9.2-87.6mm (mean length= 46.4mm, N=16 from 9 branchlets all less than 40cm long) and cut width varied from 1.3-3.9mm (mean width: 3.2mm). For the *E. pellita* sample (diameter 10.1-14.00mm) incised cut lengths varied from 59.6-133.00mm (mean length= 91.5, N= 6 from 4 branchlets all less than 40cm long) and cut width varied from 2.0-7.6mm (mean width 3.3mm). Cuts from both species of eucalypt had healed and calloused leaving a raised 'lip'-like ridge around a ribbon of exposed sapwood. Cicadas had oviposited in the sapwood of most of these cuts (exposed sapwood of all long incisions (i.e. 9 >50mm) in the *E. intermedia* sample and of 4 in the *E. pellita* sample). The fresh *E. intermedia* incision sites carried red kino stain on and under the calloused edges of the incision, but this was not as apparent in the *E. pellita* incisions.

A sample of bloodwood kino was taken from the branches showing fresh incisions. Preliminary analysis results were as follows: moisture 39.6%, protein (N×6.25) 1.3%. Infra-red spectroscopy showed the substance was a complex mixture consisting of polymerised and/or unpolymerised higher alcohols, probably containing carbohydrate material either in bound or free form. It was not possible to characterise these components more precisely, or to determine the proportion of apparent carbohydrate in the exudate. However no simple sugars were present in free form (N. Douglas, pers. comm.).

Although not visible from the ground, wounds similar to those described above are very common in the small branches of the canopy in *E. intermedia, E. pellita* and *E. clarksoniana* throughout the range of *P. gracilis*. As yet there are no criteria for distinguishing cuts made by *P. gracilis* from those of *P. breviceps*, which occurs sympatrically with *P. gracilis* but is not tolerated socially by it.

FIG. 19. Overlap in home ranges of adult female T4026 (_____), sub-adult female T4027 (_ . _ . _) and sub-adult female T4028 (_ _ _ _). The MCP boundaries are represented by thin lines corresponding in pattern with the respective 95% isopleth indicated by the thick, curved lines. Crosses indicate the location of the 3 dens used by adult male T4030 over 3 consecutive nights (7-9 Sept 1991). Dots indicate the only 3 dens used by adult female T4031 during the period 9-15 Sept 1991. Arrows indicate the only natural corridor connecting land north and south of the central swale. Shaded areas indicate cleared land.



Acacia arils and gum: One female (T4026) was observed on 27 Nov 1991 from 1742 hrs to 0330 hrs (28 Nov 91) (Table 6). During that time the glider, which had fully furred young in the nest, fed almost exclusively on arils of *A. crassicarpa* (Fig. 27) which it collected from gaping pods. The only other food eaten during the night was a grasshopper/katydid caught by the glider while in the process of aril feeding. Gum exudates of *A. crassicarpa* were licked and new sites on a trunk were roughly gouged and torn open.

Lichens: A female (T4026) was observed 16 Aug 1991 from 0200hrs-0230hrs feeding on lichen growing on the bark of *Lophostemon suaveolens*. The glider chipped off flakes of bark, licked the lichens off then let the bark chip fall. A sample of lichen taken from the feeding site contained only clonal reproducing bodies (soredia) and was unidentifiable (R. Rogers, pers. comm.).

Psyllids and honey dew: A female (T4026) was observed on 13 Aug 1992 from 2000-2130hrs feeding on the psyllid *Eriococcus* sp. (Fig. 28) which had infested the underside of leaves in the canopy (at 10m) of an *E. pellita* (Table 6). The glider appeared to scrape and lick psyllids off the leaves' mid-vein. Results of preliminary analysis of scale insects are as follows: moisture= 55%, lipids= 13.2%, protein (N×6.25)= 20%. Of the

FIG. 20. Nestling young of female T4026 (T4032 and T4033) photographed 26 Nov 1991.

13.2% lipids in the sample, 6.3% could be regarded as higher molecular weight glyceride waxes and the remaining 6.9% as fatty oils. The protein figure was obtained by applying the conversion factor normally used for converting nitrogen content to protein, however nitrogen would be present not only in the protein but also in the chitin. The analysis was not able to differentiate between nitrogen derived from protein and that contained in chitin (N. Douglas, pers. comm.).

A male was observed on 2 Oct 1992 licking along the underside of *E. intermedia* leaves. It appeared to consume both the psyllid *Eucalyptolyma distincta* and its lerp (Fig. 29).

A female (T4026) was observed 13 Aug 1991 licking honey dew off the upper and lower surfaces of leaves of *E.pellita*.

Other arthropods and arachnids: Large insects were usually manipulated and consumed while the glider hung upside-down by the hind legs against a tree trunk, leaving the forelimbs free to manipulate prey. In the case of a large grasshopper, the gut was dismembered and extracted by biting and holding one end of the insect in the mouth, holding the other end in the forefeet, extending the forelimbs fully, tossing the head back and thereby stretching out the gut in a long string. A female (T4026) was once observed catching a flying moth by grabbing it with the forefeet alone.

On 13 Aug 1991, a female glider (T4026) was observed tearing into an occupied arboreal nest of Green Tree Ants and for 5 minutes after, eating something taken from the nest. The act of breaching the nest was undertaken at some apparent discomfort to the glider which shook its legs and flicked ants off its body for the following 20 minutes.

The stomach of an adult male glider collected on 9 Dec 1989 while feeding in flowering *E. tessellaris* contained the remains of numerous scarabaeid beetles which, presumably, had also been feeding at the flowers.

Water: After rain, gliders were observed licking water off petioles and leaves of *L. suaveolens* and *E. intermedia*. During rain, one glider was observed to move under the protective cover of a thick semi-horizontal branch. It remained still with head down until the rain passed. This animal dried its wet tail by thrashing it from side to side.

DISCUSSION

TAXONOMY

Alexander (1981) commented that, of the recognised subspecies of *P. norfolcensis* and *P. breviceps*, *P. n. gracilis* and *P. b. longicaudatus* needed further detailed revision before they could be accepted as valid races. He noted that *P. n. gracilis* was based on one specimen from north of Cardwell, differing from the nominate subspecies in its markings, shorter ears, and a more slender tail; all features he demonstrated to be highly variable in specimens of *P. norfolcensis* from Queensland to Victoria. Had de Vis drawn attention to only those features, it could have been said that he described *P. gracilis* for all the wrong reasons. But de Vis also made a note that 'In size [*P. gracilis* was] intermediate between *B. australis* and *B. sciureus* [*P. norfolcensis*]' (de Vis, 1883: 620), a significant statement that has not received the attention due to it in the literature. The set of measurements which accompany the de Vis description lie well outside those given by Thomas (1888) for specimens of *P. norfolcensis*. The lowland Tully-Ingham gliders I have attributed to *P. gracilis* are, in size, consistent with the large dimensions outlined in the de Vis description and, by the veracity they impart to the original measurements, reinforce the suspicion that neither Thomas nor subsequent authors who also dealt with *P. gracilis* as a synonym of *P. norfolcensis* had ever made a personal examination of either the specimen de Vis described in 1883, or of any other similar glider from nearby.

In body and tail length *P. gracilis* is similar to the large New Guinean glider *P. abidi* (Fig. 5).

FIG. 21. *Eucalyptus intermedia* nest tree (Nest Site 1 of Table 4) showing entrance hole (top arrow) 3m above nest (bottom arrow).

However, dental and biochemical systematic studies (Van Dyck, 1990; Colgan & Flannery, 1992) put *P. gracilis* closest to *P. norfolcensis*. The dental morphology of *P. abidi*, in particular the unreduced nature of P^2, the unreduced protocone of M^2, and the broad ectoloph of M^2 and M^3 suggest a more pleisomorphic species from which the Australian species *P. gracilis*, *P. norfolcensis* and *P. breviceps* could have been derived.

The large size of *P. gracilis* is worth noting in the context of its close affinities with *P. norfolcensis*. Alexander (1981) concluded that Victorian populations of *P. norfolcensis* were significantly larger than those of southeast Queensland, and that the size increase from north to south was gradual and continuous, thereby representing a latitudinal clinal variation in body size which could be attributed to Bergmann's rule. All adult specimens of *P. gracilis* examined (from latitudes 18°02'-18°27') were larger in skull length (maxskull length: mean= 51.14, N= 7, SD= 0.95) than Victorian *P. norfolcensis* (mean= 47.52, N= 5, SD= 0.64) from latitudes 36°23'-38°26', and significantly larger ($P<0.001$) in body length than Victorian *P.norfolcensis* (for *P. gracilis* mean= 247.45, N= 11, SD= 15.86; for *P. norfolcensis* mean= 212.40, N= 5, SD= 16.69). This reversal in the clinal trend in *P. gracilis* is offset by normal trends attributable to Bergmann's rule seen in other possums and gliders such as *P. breviceps* (Smith, 1973), *P. australis* (Russell, 1984), *Petauroides volans* and *Trichosurus vulpecula* (Yom-Tov & Nix, 1986).

Food Selection

It is as difficult to account for the selective pressures resulting in large body size in *P. gracilis*, as it is to interpret the 'impetus for body size development' (Smith & Lee, 1984) in the entire Petauridae given the minor dietary differences between the species. Among exudivores *P. gracilis* is more of a dietary opportunist, feeding on nectar, pollen, arthropods, arachnids, wattle exudates, honeydew and eucalypt saps when these food items become seasonally available. Although similar diets have been thoroughly documented for other petaurids such as *P. breviceps* (Fleay, 1947; Smith, 1980, 1982; Suckling, 1980; Suckling & McFarlane, 1983) and *P. australis* (Smith & Russell, 1982; Henry & Craig, 1984; Craig, 1985; Goldingay, 1986, 1987; Kavanagh, 1987a, 1987b) the occurrence of other significant dietary items such as *Acacia* arils, *Xanthorrhoea* exudates, *E.intermedia* sap and/or kino, lichens and green tree ants (or the contents of their nests) has not been reported for the group.

Australian *Acacia* species have been divided into three dispersal groups (O'Dowd & Gill, 1986): 1, arillate *Acacia* that are bird dispersed (17% of 92 species sampled); 2, arillate *Acacia* that are ant dispersed (74%); and 3, the remaining non-arillate *Acacia* species (9%) that do not correlate with dispersal by ants or birds. O'Dowd & Gill showed that in bird-syndrome species diaspores (dispersal units) were as follows: predominately bicoloured, displayed in dehisced pods retained in the canopy, high in aril mass and lipid content and significantly longer and more contorted than in ant dispersed *Acacia* . Diaspores of ant-syndrome species were presented inconspicuously on the ground and investment was low.

In the broad sense, bird and ant dispersed seeds are thought to escape from interspecific competition, fire, parental competition and seed predators, and/or benefit from transportation to

FIG. 22. *Lophostemon suaveolens* nest tree (Nest Site 3 of Table 4) showing relative size of entrance hole.

microsites with superior nutrients (Holldobler & Wilson, 1990). O'Dowd & Gill (1986) considered two of these most relevant to the *Acacia* group: escape from the detrimental effects associated with the parent plant, and an increased chance of being directed to specific microhabitats by the dispersal agent. They note that in some *Acacia* species, lipids might account for 70% of the aril dry mass, a value comparable to the highest lipid contents observed in seeds and fruits. They argue that lipids provide a greater energy reward per unit mass of aril, since lipids yield roughly twice the energy upon catabolism as carbohydrates, and they conclude that since most of the known dispersal agents of *Acacia* are generalist feeders and incorporate insects into their diet, the higher proportion of saturated fatty acids may 'mimic' the saturated fatty acid composition typically found in animal prey.

Petaurus gracilis stands to gain much from the summer aril harvest provided by *A. crassicarpa*, a bird-syndrome *Acacia* whose arils, though not brightly coloured, are long (convoluted around 14mm) and prominently displayed (Fig. 27) in the canopy over many weeks. Female gliders in late lactation (December) with nestling young in dens surrounded by seeding *A. crassicarpa* might be expected to significantly reduce energy costs by foraging on arils close to the nursery den. As the gliders did not eat the *Acacia* seeds, but discarded them below the tree, it is doubtful that the tree derives anything advantageous from the relationship.

The August 1991 observation of a glider breaching an occupied arboreal nest of Green Tree Ants and for 5 minutes thereafter eating something taken from the nest, deserves comment here. Larvae were initially considered the objects of the glider's attention. However, nests breached by M. Hopkins (pers. comm.) in an

FIG. 23. New scapes of *Xanthorrhoea johnsonii* carry a 'bloom' of waxy spicules. Gliders visiting scapes leave long-lasting footprints in the wax. Surveys of *P. gracilis* habitat are facilitated by an inspection of *Xanthorrhoea* inflorescenses.

FIG. 24. *Xanthorrhoea johnsonii* scape showing tapping gouges attributed to *P. gracilis.*

unrelated study, were found to contain abundant harvested *Acacia* arils. Three *Acacia* species occur commonly in *P. gracilis* habitat: *A. crassicarpa*, *A. flavescens* and *A. mangium*. However the three species flower concurrently through May making it unlikely that mature arils would be available for harvest and storage as early as mid-August. Given the longevity of arils it is possible that the items extracted from the nest were arils harvested by the ants the previous summer.

The grasstree *Xanthorrhoea johnsonii* has a wide geographic and environmental range on the east coast, tablelands and western slopes from Cape York Peninsula south to Singleton, New South Wales (Bedford et al., 1986). Unlike most other glider sites within the surveyed area, *X. johnsonii* was common at Barretts Lagoon with densities exceeding 1000 plants per 1000m^2. There, soils were waterlogged for extended periods during the wet season, and flowering in both 1991 (a non-fire year) and 1992 (severe fire in early January) occurred from May to August. During this time both *P. gracilis* and *P. breviceps* were observed feeding (separately) on spike nectar, but only *P.gracilis* was observed tapping young scapes for exudate (Van Dyck, 1992b). As scapes and spikes matured it became difficult to distinguish between scape damage due to gliders and that caused by insects. Large crickets were noted grazing broad (5mm) shallow channels in immature upper scapes which later oozed exudate and calloused to leave scars similar to those left by gliders. As scapes further matured, a glider's bite at the base of a scape could have been interpreted as either a gum tap or an attempt to get at worm-like beetle larvae that sometimes excavated burrow networks in the lower part of the scape.

Pollen analysis showed *Xanthorrhoea* pollen intake between May and August and rhomboidal crystals of silica in the May 10 sample. The presence of the silica crystals demonstrates that

FIG. 25. *Xanthorrhoea johnsonii* spike being licked by sub-adult female *P. gracilis* T4027.

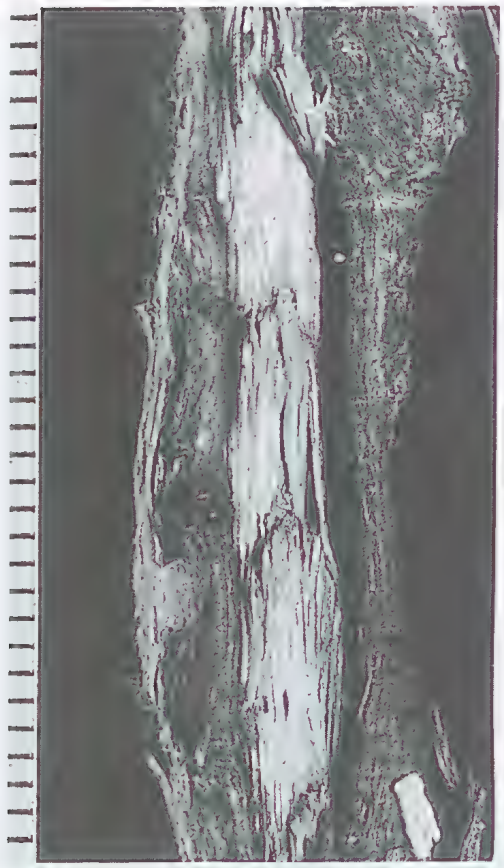


FIG. 26. Branch of *Eucalyptus intermedia* stripped for sap and/or kino by *P. gracilis*. Note cicada ovipositions.

the glider may have foraged scape tissue of *Xanthorrhoea*, as rhomboidal silica surrounds the secondary bundles of this taxon (Staff & Waterhouse, 1982). In May, a high proportion of scapes were tender and, presumably most productive when tapped. The results also suggest a high percentage (up to 70%) of *Xanthorrhoea* pollen is available for digestion through release of the contents via the aperture. *Xanthorrhoea* pollen may provide a convenient and rich source of protein by virtue of the high ratio of pollen aperture to surface area making the contents more readily available than pollen from other sources e.g. *Eucalyptus* (M. Dettmann, pers. comm.). Pollen has a high protein content (6-34%, Smith, 1982). Given the carbohydrate and protein rewards offered by *X. johnsonii* over a long period, the intake of scape exudate is noteworthy in respect of its possible digestibility-reducing or toxic secondary plant compounds. Investigations of the complex mixture of aromatic compounds found in *Xanthorrhoea* have concentrated on resins present in the trunk (Birch & Hextall, 1955; Duewell 1955, 1965, 1968; Duewell & Haig 1968) but not in the scape. Phenols and flavinoids are known components of young scapes (D. Bedford, pers. comm.) and their injestion by cattle has been attributed to poisonings during autumn and early winter in north Queensland (the sometimes fatal condition known as 'wamps' or 'crampy disease'). The toxic principle involved in such poisonings has not been investigated (Everist, 1974). Hall (1956, 1965) noted that young *Xanthorrhoea* spikes (probably *X. fulva*, D. Bedford, pers. comm.) appeared to be more toxic than old ones, and there was evidence to suggest that the scape was more poisonous than the spike.

Australian folivorous marsupials have been shown to exhibit a number of physiological and morphological adaptations to cope with xenobiotic compounds such as tannins and other polyphenols in their diets (Hume et al., 1984; Foley, 1987; Foley & Hume, 1987; Foley et al., 1987). The development of the hindgut, in particular the caecum, into a fermenting chamber, is

FIG. 27. Prominently displayed seeds and arils of the 'bird-syndrome' *Acacia crassicarpa*. This *Acacia* is an important understorey component of *P. gracilis* habitat.

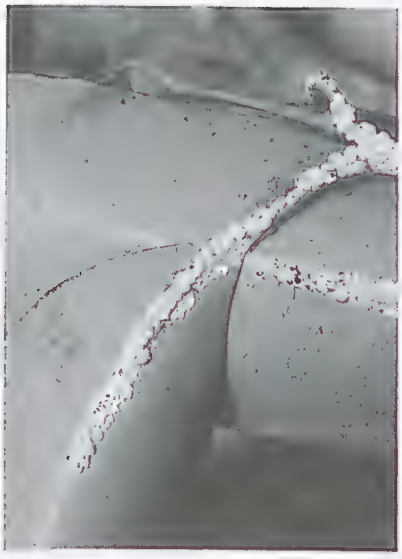


FIG. 28. *Eriococcus* sp. on *Eucalyptus pellita* foliage. Both scale and psyllid are eaten by *P. gracilis*.

one of these adaptations and its role in the bacterial fermentation of carbohydrate polymers (some plant gums) eaten by petaurids is discussed by Smith (1982a, 1982b). In external proportions, the alimentary tract of *P. gracilis* (Fig. 30) resembles that of *P. breviceps*. In one specimen of *P. gracilis* (JM7400), the small intestine (44cm) tapered gradually from 1.3cm diameter below the duodenum to 2.9cm diameter at the point of juncture with the hindgut and caecum. The caecum was 7.8cm long and broadest at 1.5cm. The colon was long (25cm). The length of the caecum in *P. gracilis* was roughly twice that (or 11.3% of total gut length) of the caecum in the striped possum *Dactylopsila trivirgata* (6.9% of total gut length, see Smith, 1982b). The colon in *P. gracilis* occupied approximately 36% of total gut length and compared to 17.2% in *D. trivirgata*. The striped possum has a similar body weight to, and occurs sympatrically with, *P. gracilis* through most of the latter's range. If this difference in the capacity of the hindgut reflects a physiological advantage in *P gracilis* to deal more successfully with the toxic polyphenols and complex carbohydrates of *Xanthorrhoea* gums and exudates, it may provide further ecological segregation between the two species.

This segregation may further be reinforced by the ability of *P. gracilis* to deal with lichens whose secondary chemicals (toxic polyphenols) may be a defense response to predation or an aggressive allelopathic response (Lawrey, 1986; Rogers, 1990) and Pink Bloodwood (*E. intermedia*) sap and/or kino (although precisely which one of these or what proportions the glider takes from branchlet slashings and small trunk wounds is not known). Old, red-stained, calloused slashings were often found to be fed by kino ducts, and did not display crusted kino on the wound, suggesting that either this type of wound may not crust over naturally, or gliders may have cleared away or eaten the crystalline form and then fed on kino liquor as it leaked into the wound. Kino, the 'blood' from which the group of 'bloodwood' eucalypts are renowned and named, is astringent to taste and contains large quantities of toxic polyphenols (Smith, 1982). The results of chemical analysis of Pink Bloodwood kino from Barretts Lagoon suggested broad superficial similarities to *Xanthorrhoea* exudate. Gliders of any species have not previously been reported to feed on kino.

Phloem sap feeding is well documented for *P.*

FIG. 29. *Eucalyptolyma distincta* on *Eucalyptus intermedia* foliage. Both lerp and psyllid are eaten by *P. gracilis*.

FIG. 30. Dissected gut of *P. gracilis* (JM7400).

breviceps and *P. australis* (see previous references). Smith (1982) noted that when gliders fed on sap they were generally seen to chew the sides of the wound and Craig (1985) described bark stripping in *P. australis* where bark and adhering conducting tissues of both *E. cypellocarpa* and *E. obliqua* were stripped to a depth of 1-2mm and torn free in long slivers, which were immediately discarded and the damaged surface licked intensively. It is possible that similar gouging behaviour observed in *P. gracilis* in the canopies of both *E. intermedia* and *E. pellita* was directed at phloem sap and not at kino. In that no actively worked sap-site trunks such as those characteristic of *P. australis* were detected over the course of the survey, it may be that for *E. intermedia* at least, thin canopy branches provide the most convenient access to phloem sap where trunk gouging might be too quickly counteracted by a kino injury response. Given the critical importance of the northern bloodwood complex (*E. intermedia*, *E. clarksoniana*, *E. dolichocarpa*) to the distribution of *P. gracilis* (see below), the shortcomings associated with knowledge of this glider's relationship with these species need to be addressed. Given its relatively large size, *P. gracilis* may be dependent on this group for incising and thereby the geographic range of the glider is, in part, determined by the presence of these trees.

Distribution and Habitat

Sites supporting *P. gracilis* are characterised by very high (seasonal) precipitation and a woodland vegetation blend that is shaped and maintained by fire. The glider's narrow range coincides with the wettest zone in Australia (Tully's mean yearly total rainfall is 4188mm). Coastal areas at the southern limit of the *P. gracilis* range may appear suitable in habitat (e.g. Clemant State Forest 34, near Rollingstone) yet fail to support petaurids other than *P. breviceps*. Large, mature woodland trees of the coastal ridges and plains (e.g. *E. intermedia*, *E. pellita*, *L. suaveolens*) are shallow-rooted, and although trees in such low-lying areas are subject to protracted periods of seasonal inundation, their sandy soils also drain quickly and thoroughly during the extended winter-spring dry season. It is most likely that the ultimate climatic parameter determining the distribution of *P. gracilis* is a dry season moisture threshold (probably close to 100mm dry quarter precipitation) below which its moisture demands cannot be easily satisfied.

Ironically, the high rainfall requirement which partly determines the glider's presence in an area also potentially undermines its long-term survival prospects. Many dryland communities suitable to *P. gracilis* are actively evolving from sclerophyll to vine forest because of changing fire regimes (P. Stanton pers. comm.). Traditional burning practices no longer operate in the area and the threat of economic loss through damage to sugarcane and pine plantations acts as a discouragement to burning-off in adjoining woodland areas. This is linked to a public perception that fires are a 'bad' thing and rainforests are 'best'. Rapidly evolving rainforest communities

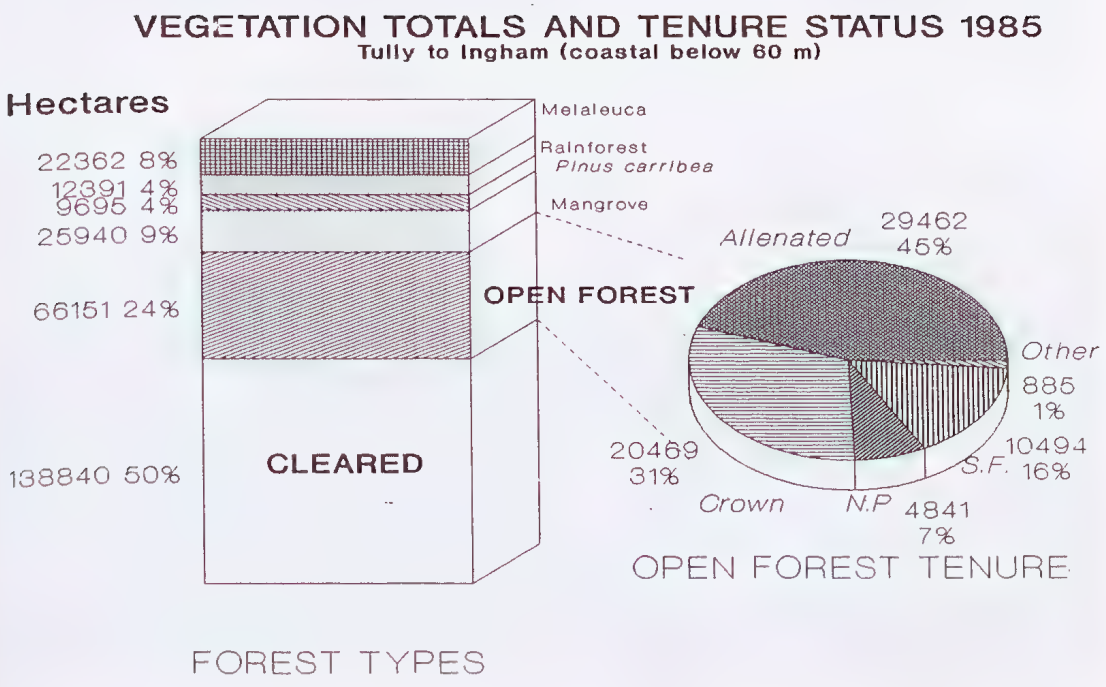


FIG. 31.The status of vegetation types (in general) and open forest (in particular) throughout the range of *P. gracilis*. For coverage see Fig. 1 (Smiths Gap south to Bambaru). Figures supplied by Queensland Forest Service.

were noted in woodlands at the Hull River site, Edmund Kennedy National Park, Murray Upper, Hinchinbrook Is. and parts of Barretts Lagoon.

Petaurus gracilis is dependent on mature stands of mixed-species remnant woodland. The presence of at least one of the 'bloodwood' group (*E. intermedia*, *E. clarksoniana*, *E. dolichocarpa*) and an accompanying species of bird-syndrome *Acacia* (usually *A. crassicarpa*, less often *A. flavescens* or *A. mangium*) is suggested as a minimal basis for suitable habitat. In a few cases, the place of a bloodwood might be taken by *E. pellita*. This species flowers heavily in February and March, coinciding with bloodwood flowering. Hypanthums of *E. pellita* blossoms range from 6-10mm, and gliders have been observed to spend entire nights feeding in individual trees (see Goldingay, 1987, 1989 for similar behaviour in *P. australis* at single sap-sites). The presence of *E. pellita* was considered to indicate areas of high quality glider habitat. Where mature *E. pellita* combined with *Xanthorrhoea johnsonii*, the resultant habitat blend could often be regarded as optimal (e.g. areas of Barretts Lagoon). Habitat considered sub-optimal was characterised by a trend toward species-poor assemblages and dominance by a single eucalypt species e.g. *E. platyphylla* (Wharps Holding), *E. clohesiana* (Hinchinbrook Is.), *E. intermedia* (Graham Range National Park). A curious human bias toward leaving mature *E. tereticornis* in cultivated paddocks and narrow belts along roadsides (e.g. Kennedy Valley, Ashton and Lannercost Creeks) has meant that gliders can often occupy heavily degraded and fragmented habitat where vestiges of suitable riparian (gully) habitat provide summer requirements. *Eucalyptus tereticornis*, a mid-winter flowering species is known as a major source of winter pollen and a useful source of nectar (Penfold & Willis, 1961; Chippendale, 1988). Also the presence of many large mature specimens of *Deplanchea tetraphylla* distributed sparsely but evenly throughout the glider's range is considered important in that they provided an abundant source of nectar (and perhaps pollen) at a time (August, September) when little else is in flower.

Social Organisation and Home Range

The small sample size upon which these comments are based should not be ignored. Barretts

FIG. 32. Lowland woodland clearing for *Pinus carribea* plantations has accounted for a loss of at least 9,695ha of *P. gracilis* habitat. In late 1992 Queensland Forest Service suspended clearing of native forests near Cardwell following the recording of *P. gracilis* in foothill remnants at Porters Creek (shown here overlooking Hinchinbrook Is.).

Lagoon, where a total of five gliders were radio-tagged, included patches of habitat considered optimal for *P. gracilis*. The woodland community was structurally complex with abundant species of *Eucalyptus* (4), *Melaleuca* (4), *Acacia* (4) and with a dense understorey of *Xanthorrhoea*. The availability of diverse sources of carbohydrate and protein throughout the year (see Table 6), combined with an abundance of nest sites, could be expected to be reflected in a polygynous mating system (Emlen & Oring, 1977; Lee & Cockburn, 1985; Henry, 1984; Goldingay, 1992) as polygyny in the Petauridae is thought to evolve when resources are abundant enough for male gliders to defend a territory which can support more than one female consort. However, *P. gracilis* appears unconventional in its pattern of social organisation. The two adult females in this study had home ranges that appeared to be relatively exclusive of one another (Fig. 19). Two dispersing sub-adult females were largely solitary although their home ranges overlapped consistently with one another and with one of the adult females (presumed to be their mother). The adult male denned either alone or with either solitary adult female and regularly spent time with at least one of them for part of the night. This system is a departure from the nature of polygynous mating systems generally attributed to either *P. breviceps* (polygynous: Smith, 1980; Suckling, 1980) or *P. australis* (monogamous: Craig, 1985; Goldingay & Kavanagh, 1990; polygynous or monogamous: Russell, 1984; Goldingay, 1992). The apparent system in *P. gracilis* more closely approximates that seen in *Petauroides volans* (Henry, 1984; Kehl & Boorsboom, 1984), although the home range is much larger in *P. gracilis* (23ha for an adult female compared to 1.25-2.5ha in a *P. volans* female), and the investment in female and/or resource defense by male *P. gracilis* could be anticipated to greatly exceed that by male *P. volans*.

It is tempting to draw similarities between the social behaviour of *P. gracilis* and that of the tropical African exudivorous prosimian *Galago senegalensis moholi* as reviewed by Bearder

TABLE 6. Food items recorded for *P. gracilis* by direct observation.

Food item	Source	Month recorded	Locality (from Table 1)
Nectar and pollen	Blossoms of:		
	E. pellita	Feb, Mar	7, 14, 15, 19
	E. clarksoniana	Mar	6, 14
	M. elleryana	Mar	9
	X. johnsonii	May	19
	A. crassicarpa	May	19
	E. tereticornis	Jun	5, 19
	D. tetraphylla	Aug	19
	M. dealbata	Oct	19, 1
	E. tessellaris	Nov	19
Incision exudates	A. crassicarpa	May	19
	X. johnsonii	May	19
	E. intermedia	Sep	19
	E. pellita	Sep	19
Acacia arils	*A. crassicarpa*	Dec	19
Lichen	*L. suaveolens*	Aug	19
Spiders/Insects	large (?huntsman) spider	May	19
	cockroach/beetle	May	19
	green ants or nest contents	Sep	19
	moth	Sep	19
	grasshopper/ katydid	Dec	19
Psyllids and lerp			
Erriococcus sp.	*E. pellita*	Aug	19
	E. intermedia	Aug	19
Eucalyptolyma distincta	E. intermedia	Oct	20
Honey dew	*E. pellita*	Sep	19

(1987). In *G. senegalensis moholi*, female territories are large enough to support feeding throughout the year and in homogeneous habitat, home ranges of females are approximately equal in size. Females signal territory ownership to conspecifics by scent marking and vocalisation; only adult females are repulsed. At first an adult daughter may share her mother's terrritory, but later there is less overlap although related females may share critical resources (up to 4 adult *P. gracilis* were once recorded feeding simultaneously in a single flowering *E. tessellaris* at Barretts Lagoon). Territories of male *G. senegalensis moholi* (i.e. 'A-males', which are older, heavier and territorial and have preferential contacts with females) overlap those of one or more females. A-male territories are signalled by scent and vocalisation and other adult males are repulsed. There is no relationship between male territory size and dietary requirements. A special bond of familiarity links a territorial male to his females. This bond is serviced by regular visits that involve direct contact with the females. The direct contact may be prolonged (several hours). Additionally, calling and indirect contact using scent marking may be employed. Male stability and territoriality depends on the presence of females. Male-male and female-female territories (between matriachies) have zones of overlap where territorial signals are exchanged.

Bearder (1987) notes that such a strategy in *G. senegalensis moholi* ensures the even spacing of single females or matriarchies throughout areas of suitable habitat and ensures that the nature of male territoriality ensures mating access to females without wasting energy on subordinates. Smith & Lee (1984) comment that theoretically, female possums might be expected to obtain more nutrients for survival and reproduction when solitary (and defending solitary territories) except when specific advantages of clumping outweigh the disadvantages of sharing resources. Given the combination of its moderately large size, and the benign tropical climate associated with its habitat, *P. gracilis* could be expected to have a low relative cost of thermoregulation and as a result it may avoid group huddling.

The threat from Rufous Owls (*Ninox rufa*) and Lesser Sooty Owls (*Tyto multipunctata*) which occur commonly throughout the range of *P. gracilis* may also make lone foraging a response to crypsis for defense (Henry, 1984, for this behaviour in *P. volans*). Of 5 regurgitated pellets retrieved from a Rufous Owl's nest site at Lannercost, 1 pellet contained maxillary fragments of an adult specimen of *P. gracilis*.

The Barretts Lagoon situation may reflect an artificial situation in that the adult female home ranges were separated by an extensive treeless swale with one narrow natural corridor connection at the southern end (Fig. 19). The western side of one of those home ranges was bordered by a road. Investments in female resource defense by the male may have thereby been greatly reduced, and elsewhere, in areas of more contiguous habitat, *P. gracilis* way prove to exhibit a mating system compatible with that described for other petaurids.

If the mating system at Barretts Lagoon was

typical, the quasi-polygynous system may offer abundant resources of food and time to reproductive males, yet just sufficient resources for reproductive females to feed themselves, and tolerate two, large, weaned young (and perhaps a second litter) dispersing slowly from the female's home range. The use by females of multiple dens scattered throughout the home range may represent a cost effective method of territory defense. Home range size and mating strategy have been shown to vary in *P. australis* with the productivity of the site (see Goldingay, 1992 for review). It is likely that in marginal to poor habitats (e.g. Wharps Holding), the sociecology of *P. gracilis* will vary from that of Barretts Lagoon.

Conservation Status

Most records of *P. gracilis* (Table 1) have come from altitudes below the 60m contour (mean altitude= 17m; SD= 19.8; SE= 0.35; N= 57). The total area encompassing site records to date of *P. gracilis* is shown in Fig. 31. Of this total area which amounts to 438,454ha, approx. 63% (275,379ha) occurs below the 60m contour. Of this lowland vegetation approx. 50.4% (138,840 ha) has been totally cleared of forest through primary production (mainly establishment of sugar-cane, cattle, bananas, pineapples, fruit trees, aquaculture), logging, and the cultivation of *Pinus carribea* in plantations (9,695 ha) since 1967. The balance of open forest which totals approx. 66,151ha and represents a surviving approx. 20% of the original component of lowland open forest (P. Stanton, I. Robb, pers. comms), is highly fragmented, the subject of ad hoc fire regimes and mostly unprotected. Approximately 76% of this remnant is potentially available for future development (45% alienated (i.e. freehold/leased), 31% Crown). *Petaurus gracilis* is poorly represented in the 7% (4841ha) open forest protected by National Park tenure (see preceding), and the remaining significant slice of 16% (State Forest, 10,494ha) is highly fragmented. In late 1992, Queensland Forest Service (QFS) suspended clearing of native forest near Cardwell following the recording of *P. gracilis* in State Forest at Porters Creek. Seven specific areas of the coastal lowlands had been selected by QFS for clearing prior to the establishment of exotic pine plantations (total area 3710 ha). Each area was investigated by the QFS Fauna Conservation and Ecology Section in October 1992 to determine the presence of *P. gracilis* and to allow an evaluation of the conservation significance of each proposed area as *P. gracilis* habitat. Gliders were detected in 4 of the 7 sites investigated (total area 3050ha) and in locating gliders at Wharps Holding, QFS ecologists extended the known southerly distribution of the species (J. Kehl, pers. comm.).

Core areas predicted by the BIOCLIM system have been mostly cleared from the north and south and replaced along the Ingham-Tully coast by plantation pine (Fig. 32). Records from predicted marginal areas indicate the present day distribution is concentrated near foothills and relictual riparian corridors. The extensive area east and south of Barretts Lagoon represents a significant remnant core area.

The endangered status of *P. gracilis* (Van Dyck, 1991) in tropical Queensland should not be regarded in isolation, but seen as symptomatic of a pattern of decline of abundance and extinction repeated across Australia. The threats faced by this glider are not unique to it but shared by the entire tropical coastal lowland woodland ecosystem of which it is one component. In 1982, Tracey commented that his Vegetation Types 18 (Swampy Coastal Plains) and 19 (Coastal Floodplains and Piedmont Swamps) had been either cleared and drained for sugar-cane, or where they had once been common along the Tully River and Murray River were now practically extinct. Braby (1992) reviewed the status and biology of eleven species of butterfly dependent on the Cardwell Basin lowland woodlands and concluded that their habitat ranked among the most threatened habitats in north Queensland. Recher & Lim (1990) presented data suggesting that the decline of vertebrates first observed in southern Australia has extended to the northern parts of the continent and that fauna of the wetter coastal regions may also be affected. They predicted that if such observations are correct, the outcome will be the rapid extinction of species throughout Australia in the next few decades. They recommend that in the conservation of terrestrial fauna, the emphasis needs to shift from species preservation to the management of ecosystems.

'The scale of change is not of individuals or populations, but of functional units of interacting organisms. Once destroyed it is no more likely that an ecosystem can be restored to its original state than an extinct species can be resurrected from its bones recovered from a museum drawer' (Recher & Lim, 1990: 295).

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TABLE 7. Macerals and pollen types identified in faecal samples of *P. gracilis* from Barretts Lagoon, 1991. Frequency: H = high, M = moderate, L = low. Abundance: A = abundant, C = common, R = rare.

Slide contents	Feb	10 May	6 Aug	9 Aug	26 Nov
CONTROL SLIDE (maceral type)					
Pollen	M	L	H	L	M
Other plant mat.	M	H	M	H	H
Insect fragments	M	L	M	M	L
Silica crystals		L			
% pollen with contents	40	50	30	20	20
POLLEN SLIDE (pollen type/ abundance)					
Myrtaceae	A	R		A	A
Banksia		C			
Xanthorrhoea		C	A	C	
Grevillea/Hakea				R	
Acacia				R	

Cook University) who were prepared to work, to be paid, and to smell like slaves during the field component of this survey. Their monumental effort is warmly acknowledged.

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THE PRODUCTION AND DISPOSAL OF PIGS BY KUBO PEOPLE OF PAPUA NEW GUINEA

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Dwyer, P.D. 1993 06 30: The production and disposal of pigs by Kubo people of Papua New Guinea. *Memoirs of the Queensland Museum* 33(1): 123-142. Brisbane. ISSN 0079-8835.

In 1986-87, a small community of Kubo people, of the interior lowlands of Papua New Guinea, kept from 0.27 to 0.54 domestic pigs per person. The animals were fathered by wild boars and born to both wild and domestic sows. Male pigs were castrated. For about 18 months each pig was in the care of a particular woman; thereafter, it was released to forage in the backswamps but was regularly monitored by its carer and, like village-based pigs, provided with much fodder, particularly the pith from sago palms. An exceptionally close bond was established between each domestic pig and its carer. Men contributed little to the management of domestic pigs, and carers participated actively when pork from pigs that had been in their charge was distributed. Domestic pigs were not important as a protein source. Their significance was primarily social. On several counts, patterns of production and disposal of pigs by Kubo did not conform to expectations based in earlier comparative and theoretical analyses of New Guinean procedures. Kubo patterns are located within a comparative frame that concerns ratios of pigs to people, work entailed in maintaining pigs, nutritional matters and gender roles. □ *Socio-ecology, animal husbandry, domestic pigs, nutrition, protein, gender roles, Kubo, Western Province, Papua New Guinea.*

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Domestic pigs are important to most New Guineans. They are often focal in the social exchanges that connect different groups of people and, through the time and labour entailed in management, significant in the ecological exchanges that connect people with environment (e.g. Morren, 1977; Rubel & Rosman, 1978). These linked dimensions of the role of pigs were made clear in Rappaport's (1968) classic study among Tsembaga Maring. Indeed, in recent literature that addresses questions of social and agricultural evolution within New Guinea, the place of pigs is central (e.g. Feil, 1987; Kelly, 1988; Bayliss-Smith & Golson, 1992).

Despite the importance of pigs to both New Guineans and anthropological theorists there are few studies that include substantive detail of the husbandry practices of specific groups of people (cf. Boyd, 1984). Notable exceptions are Rappaport (1968), Hide (1981), Boyd (1984, 1985) and Kelly (1988) but these do not capture the full diversity of New Guinean pig-keeping practices (cf. Baldwin, 1990; Yen, 1991). Without an appreciation of that diversity the value of comparative analysis and evolutionary speculation will remain limited (Hide, 1981: 563).

This paper describes the production and disposal of pigs by a small group of people living in the interior lowlands of the Western Province of Papua New Guinea. These people are horticulturalists who, on the basis of extrapolating from earlier theoretical literature (e.g. Morren, 1977; Watson, 1977; Modjeska, 1982; Feil, 1987; Kelly 1988; Baldwin, 1990) might have been expected to keep few pigs or none at all, rear only wild-born piglets, raise them on forage rather than fodder, devote very little time or effort to their maintenance and use them to meet nutritional rather than social needs. Kubo people did not conform to these expectations.

KUBO PEOPLE

About 450 speakers of the Kubo language live north and northwest of the Government station at Nomad, Western Province, immediately south of the Muller and Blucher Ranges (Fig. 1; Dwyer, Minnegal & Woodyard, 1993). Between August 1986 and November 1987, with Monica Minnegal, I lived with 25 people at the village of Gwaimasi (5°54'S, 142°6'E; 80m ASL) on the west bank of the Strickland River. Our research embraced all aspects of the socio- ecology of the people and earlier reports provide details of environment, subsistence, social life and the historical context within which we worked (e.g. Dwyer & Minnegal, 1991a,b, 1992a). Details of the composition of the village population are available in Dwyer & Minnegal (1993). Here, I summarize

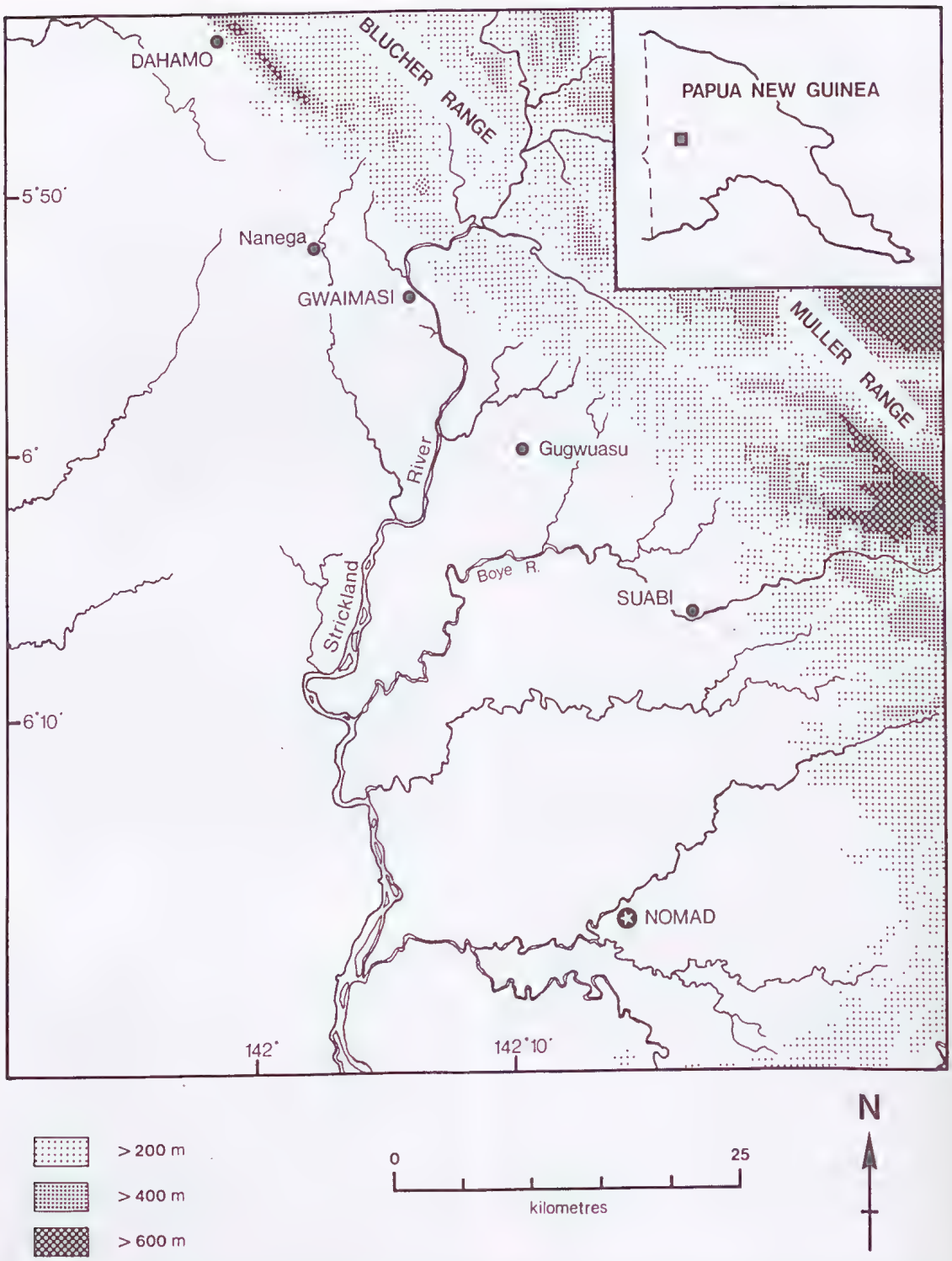

FIG. 1. Location of Gwaimasi and neighbouring communities. The large symbol shows the Government station at Nomad. Small symbols show villages mentioned in the text; names of Gwaimasi and neighbouring mission stations are capitalized.

information that is relevant to reporting matters about domestic pigs.

Gwaimasi village was centrally located within 50km^2 of foothill rainforest and swamp forest that was drained by numerous streams and the Strickland River itself. Within this area the residents of Gwaimasi produced their food. Rainfall was approximately 6m per year with recorded monthly falls never less than 300mm. The people grew bananas at small unfenced gardens made on levee banks of the river and larger streams, and extracted sago flour from both planted and wild *Metroxylon* palms that were abundant in the backswamps. These carbohydrate foods were of approximately equal importance though at different times one or the other was dominant.

Most protein was derived from animals. Wild pigs and catfish contributed most protein, in terms of weight, but many other vertebrates and invertebrates were included in the diet. Forest products, other than animals, were used as food (e.g. fern fronds, fungi, wild yams and the fruit, nuts and leaves of certain trees) and to fulfil many material needs (e.g. clothing, building and the manufacture of hunting equipment and canoes). Despite the apparent commitment, encouraged by Government and Mission contact, to establish and live in villages Kubo people remained very mobile both within and between local subsistence zones. At Gwaimasi, family groups spent long periods living at forest and garden houses away from the village and often, at these times, had little or no access to garden produce. Since about 1960 there appears to have been increased emphasis upon gardening and less emphasis upon sago extraction to satisfy calorific needs (Dwyer & Minnegal, 1992a).

Dogs and pigs were kept as domestic animals by Kubo. There were nearly as many dogs as there were people and the animals were essential to the successful pursuit-hunting of wild pigs. Domestic pigs, the subject of this paper, were less numerous. My concern here is with what Hide (1981: 406-407) called the 'ecological population': the domestic pigs cared for by a localized group of people within the area that the people themselves routinely traversed. This population need not be identical with the 'sociological population' which comprises the domestic pigs owned by a localized group of people irrespective of where those pigs are located. In New Guinea this distinction is necessary because agistment of pigs is common.

I classed domestic pigs as either 'tended' or 'free foraging'. Pigs in the former category were under almost daily supervision and spent nearly every night at or near the houses where their carers slept. Pigs in the latter category had been released to forage alone in the backswamps. At different times during its life a pig might qualify as 'tended' or as 'free foraging'. Sometimes a 'tended' pig failed to return to the village for several successive nights. Analyses presented here do not reclassify these cases as 'free foraging'; categorization as 'tended' or 'free foraging' takes the *intention* of the pig's carer to be primary. A recalcitrant 'tended' pig simply increased the work load of its carer who now had to search for it. 'Primary carers' are defined as women who had primary responsibility for particular pigs, wherever those pigs were located, and 'secondary carers' as people who were in charge of pigs for which they did not have primary responsibility. People were classed as carers of 'tended' pigs only if they had been responsible for those pigs through the day and following night. Brief periods of assistance provided during the day are not included in the analyses though they were common. Public perceptions were such that there was no ambiguity concerning the identity of primary carers of 'free foraging' pigs. My classifications of domestic pigs as 'tended' or 'free foraging' and of carers as 'primary' or 'secondary' conform closely with Kubo perceptions.

Most of the data reported below were obtained by monitoring the activities and locations of people and pigs, by direct observation of circumstances of disposal and by asking questions. Estimates of pig weight should be regarded as rough approximations. I did not have direct access to domestic pigs for measurement; the people, but not the pigs, would have tolerated this intrusion. However, where possible, wild pigs were weighed after they were killed and, before weighing, I could usually judge the weight to within 10 percent. Sixteen wild pigs with a weight range from 1.5 to 74.5kg yielded the following relationship between weight (W = intact weight in kilograms) and mandible length (M = length of horizontal ramus of mandible in millimetres): log.W = 2.91log.M - 5.07. In a few cases this formula was used to estimate the weight of domestic pigs; values obtained in this way are underestimates because domestic pigs were usually fatter than their wild counterparts. Edible weights were estimated as 0.65, 0.70 and 0.75 of intact weight for, respectively, pigs heavier than 10kg, between 5 and 10kg, and less than 5kg.

THE PIG POPULATION

Between September 1986 and November 1987 from seven to 13 domestic pigs were managed by residents of Gwaimasi (0.27 to 0.54 pigs/resident; Fig. 2). These values include piglets only from the date they were removed from sows and taken into the care of women. Piglets that were either eaten (n = 13) or exported beyond the Gwaimasi area (n = 1) on the day they were taken from a domestic sow were not counted as members of the population.

In September 1986 there were five sows and four large males; four of these animals had been born to domestic sows, the status of the others is not known. Three of the males were confirmed as castrates and the fourth was probably a castrate. One of the sows and two of the males were alive in November 1987. All recruitment during the period of study was as small piglets; five born to local domestic sows, three born to wild sows and one as an import from a neighbouring community. Males and females were included among the recruits but details are incomplete. Losses from the population were four natural deaths at estimated weights of 1.0, 1.5, 4.0 and 12.5kg and seven pigs (15-80kg) killed by people; only the latter were eaten.

Peak biomass of the pig population was in December with about 20kg live weight per resident (Fig. 2). Removals for consumption in January and March halved this value and the combination of additions, estimated growth and losses through the next 7.5 months resulted in only a minor increase in per-person biomass.

MANAGEMENT OF PIGS

At Gwaimasi, all pigs, from the time they were taken from sows, were in the care of women. The 'caring' role was unevenly distributed among available women and was strongly connected with their current reproductive status (Table 1). Caring for pigs was incompatible with caring for a nursing infant. Thus, Wafu and Gogoi did not have 'tended' pigs, Mabei's 'tended' pig was killed six months before she gave birth and the 'tended' pigs of Kose and Bowa were cared for by other women from shortly before Kose and Bowa gave birth, to several weeks after their infants died. The perceived danger to small infants arose from the possibility that pigs might consume body wastes and proximity between pigs and babies was avoided both at the village and in the forest. (Kubo people believed that an infant's health was placed at risk if its body wastes were eaten by pigs.) Carers assumed the primary responsibility for this, though, in the forest, mothers disposed of their infants' wastes and, at the village, one couple enclosed the area beneath their house so pigs could not reach wastes that might fall through the slat floor. In fact, pigs were not allowed to wander at will within the village area[1].

The married but childless woman Sisigia participated actively as a carer but it was the widow Gogo who contributed most (i.e. 41% and 64% of days associated with the care of 'tended' and 'free foraging' pigs respectively). As a widow who was probably postmenopausal Gogo's lack of direct association with nursing infants was more certain than that of any other woman. One teenaged girl ceased caring for a young pig at the time of her departure from the village to marry and another, who came in marriage, did not assume the role during the following 10 months. The caring role may have been constrained during early marriage.

The foregoing depicts differential patterns of responsibility but does not reveal the varied nature or extent of those responsibilities. I turn to these matters here, summarizing developmental events in the life of domestic pigs and the work associated with their care.

Domestic sows were impregnated by boars that lived in the backswamps. Of six successful matings, three occurred after our arrival; two of these latter were to a 'free foraging' sow and the last was to a 'tended' sow. The last case shows that insemination by wild boars did not require that sows were managed as 'free foraging' animals (cf. Kelly, 1988: 155).

When births were expected, carers or their agents monitored the sow regularly or, if it was a 'tended' pig, released it into the backswamps or remained with it away from the village. Neither pigs nor women gave birth at the village. Most piglets were captured and either killed or retained when they were from two to four weeks old. In one case a piglet was allowed intermittent access to its mother for a month after capture and, in

[1]Monica Minnegal and I visited Gwaimasi for six weeks in October and November 1991. During the first four weeks there were no children under three years and two large 'tended' pigs often wandered free near the edge of the village clearing. A child was born on November 12, 1991 and, from that time, the pigs were always tethered when mother and child were present.

another, a piglet was left with its 'free foraging' mother for six or seven weeks before it was killed and eaten. Management procedures of these kinds could inhibit return to oestrus by sows and, hence, allow some control over the timing of pregnancies (cf. Hughes & Varley, 1980: 149-151).

Capture of piglets born to domestic sows entailed an overnight stay away from the village by four to six people (female and male) together with some dogs. The presence of dogs resulted in the immediate death of some piglets and injury to others. One badly injured piglet failed to eat sat-

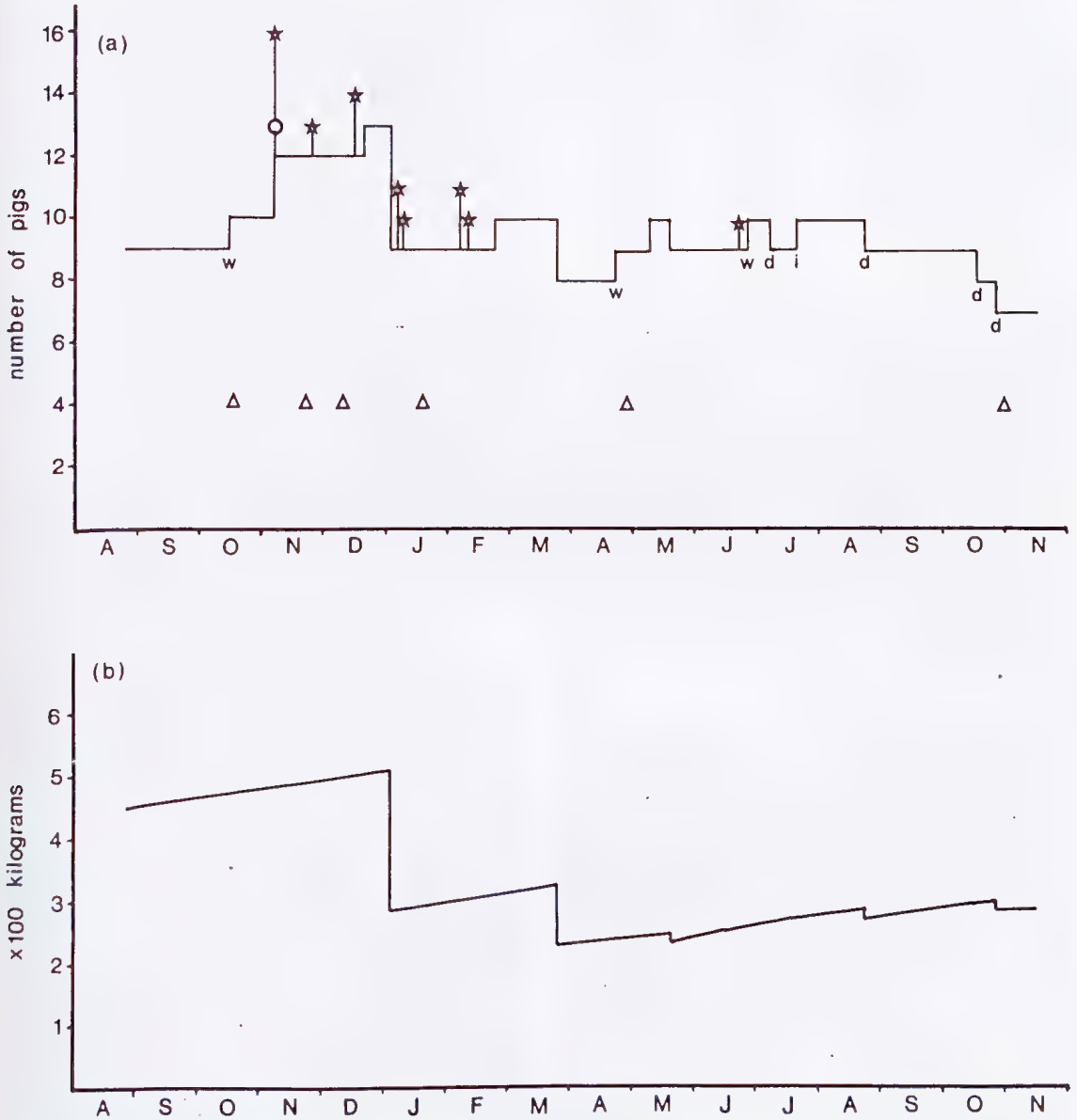

FIG. 2. (a) The size and (b) approximate biomass of the population of domestic pigs; August 1986 to November 1987. In section (a) vertical lines terminating with a star indicate piglets that were captured from domestic sows and killed and eaten on the same day; the open circle indicates one piglet that was exported on the day of capture. 'w' denotes recruitment of piglets born to wild sows, 'i' denotes an imported piglet, 'd' denotes natural deaths and open triangles record the approximate dates on which domestic sows farrowed. Capitalized letters on the horizontal axes code consecutive months.

TABLE 1. The cumulative numbers of days spent caring for pigs by female residents of Gwaimasi: August 25, 1986 to November 15, 1987[1].

		Tended pigs					Free foragers
Female[2]	Age[3]	1o carer		2° carer		total	1° carer
		village	forest	village	forest		
Gogo	45	650	327	31.5	6	1014.5	1005
Kose	40	177	84	2	—	263	26
Sisigia	30	330	141	12.5	—	483.5	—
Mabei	25	86	17	6	1	110	441
Gogoi	22	16	—	12	—	28	90
Wafu	20	—	—	10.5	13	23.5	—
Bowa	20	239	156	60.5	15	470.5	—
Yasobidua	15	—	—	—	2	2	—
Mugwa	14	68	31	4	—	103	—
Total		1566	756	141[4]	37	2500	1562

1. Values are partitioned according to the status of pigs as 'tended' or 'free foraging', as village-based or forest-based in the case of 'tended' animals, and as associated with a primary or secondary carer. All effort associated with pigs classed as 'free foraging' is attributed to primary carers though this does not accurately represent the facts (see text for further details). Half values appear in the table because two women sometimes shared the role of secondary carer. Details are not known for 173 carer-days.
2. Kose gave birth on June 10, 1987 and the child died on July 11, 1987; Mabei gave birth on July 1, 1987 and was lactating thereafter; Gogoi was lactating throughout; Wafu gave birth on January 9, 1987 and was lactating thereafter; and Bowa gave birth on July 9, 1987 and the child died the same day. Yasobidua became a resident of Gwaimasi on January 30, 1987 and Mugwa's residency ceased on the same day. The following values record the numbers of 'tended' and 'free foraging' pigs attributed to each primary carer followed by the maximum number of pigs in care at any one time: Gogo 6,3,6; Kose 2,0,2; Sisigia 2,0,2; Mabei 1,1,2; Gogoi 0,1,1; Bowa 2,0,2; Mugwa 1,0,1. When Mugwa departed from Gwaimasi her pig was transferred to Gogo's care.
3. Ages, in years, are estimates only.
4. The caring role was attributed to a visiting woman on one day and to the husband of a primary carer on another.

isfactorily and grew exceptionally slowly during 6.5 months after capture.

For more than a year after capture, pigs were closely associated with carers. For a week or two they were carried, often but not always in string bags, and petted and kissed by their primary carer and other females. From the outset they were trained to accept a lead attached to one front leg and, within a few weeks, would be led to and from the village and allowed to run free when in the forest. But intermittent carrying often continued for three months or more, by which age young pigs had been personally named and were sometimes tethered alone or near another pig in the forest. At about four and a half months their ears and tail were cut and males were castrated, and not until about five months did they spend a day foraging in the forest near the village untethered and unaccompanied by their carer. As long as they remained 'tended' pigs they were usually taken from the village on a lead though, when older than one year, they might often return unattached in the evening.

The precise timing of the events described varied between both piglets and carers. Piglets that grew slowly were treated as though they had aged slowly and some carers were more inclined than others to reduce effort by hastening the independence of pigs. Piglets usually slept in the house of their carer for the first three or four months after capture and were then tethered at night under the house. But, in one case, this bond was not broken until nine months and then only after the carer's husband became seriously ill. Women who prolonged a close attachment to pigs were also more inclined to punish misbehaviour by shouting and smacking: children were never punished in these ways unless, as infants, they defaecated in public.

The bond between pigs and their carers was strong and the effort entailed was considerable. The strength of the bond is evidenced by the minor involvement of secondary carers (Table 1) and by the facts that secondary carers were more likely than primary carers to be resident at the village (79% vs 66%; $P<0.01$) and less likely than

primary carers to take the pig to the forest to forage (56% of 68 vs 91% of 597 recorded days; $P<0.001$). When pigs that usually free foraged were located at the village secondary caring was rare (one in 52 observed days) and even the primary carer was unlikely to take the pig into the forest (two of 51 days). Other people's large pigs were difficult to manage; only after about a week of close attention from a secondary carer did even a moderately large pig become manageable.

At the village, carers were responsible for keeping pigs away from the central village area and from small household gardens, for tethering the animals at night and for matters of hygiene (e.g. cleaning sleeping quarters and removing faeces that were dropped when pigs were taken through the village to the forest). Ropes, made from the bark of trees, were made for tethering and as leads and the animals were often groomed by their carer. The pigs also had to be fed. Fodder was usually provided both in the morning and the evening. In addition, pigs were often taken to the forest where they might be tethered, accompany the carer at her pace (on or off a lead) to a place where she intended working or released to forage alone. Pigs were also 'herded', meaning that a carer accompanied by a pig or pigs, travelling at their pace, either took more time than needed to reach a place (e.g. a garden) where she intended working or spent many hours in the forest for the sole purpose of allowing the pigs to forage.

The relative importance of these different management strategies cannot be quantified here beyond noting that pigs were taken to the forest on a minimum of 87% of the days when they, and their carers, were based at the village ($n = 665$). Pig management was often embedded in other activities undertaken by carers and different carers favoured different strategies. Two women who often worked at gardens near the village favoured forest tethering; four others who worked at more distant gardens favoured other strategies. Their preferences were probably influenced by the risk that untethered pigs might return to the village and raid household gardens.

Bananas and the pith (*woko*) from sago palms were the staple fodder provided to 'tended' pigs. (Very occasionally both 'tended' and 'free foraging' pigs were fed fish. Sanio-Hewa and Gadio Enga also sometimes fed small animals to their pigs; Townsend, 1969: 50; Dornstreich, 1973: 245) Women who were based at the village nearly always took their pig(s) to places where they processed sago palms; the pigs fed at the accumulating heaps of waste pith. Chunks of *woko* from these palms were carried to the village and fed to pigs at night; portions were sometimes given to women who had not worked but who had pigs. Other palms were felled as fodder for pigs and large quantities of *woko* were buried in muddy stream beds for retrieval as needed. Again, palms at which flour extraction was completed were visited by women who 'herded' pigs. During 14 months, at least five palms were felled to provide fodder for village-based pigs that, additionally, had access to waste and unused pith from 17 palms processed on behalf of people. Only once did I see sago flour fed to a pig. In this case a woman chewed sugar cane, spat the sweet extract into crumbled flour, and hand fed the mixture to a small, sickly piglet.

When bananas were abundant they were often fed to pigs. They were cooked green, usually by boiling, peeled and sometimes mashed before delivery on a platter to the pig. Between August and November 1986 banana production was low and few were fed to pigs. Thereafter, they were used often as fodder. A tentative estimate is that at least 200 bunches of bananas were fed to pigs from September 1986 to October 1987; this represents six percent of total banana production at Gwaimasi and nearly 500g edible weight of bananas per pig for each day it was village-based (Dwyer & Minnegal, 1993). I did not see ripe bananas fed to pigs, which contrasts with Beek's (1987: 19) observation that Bedamuni, who live to the southeast of Kubo, regarded ripe bananas as fit for pigs (and anthropologists!) but not for people.

The management of 'tended' pigs was less constrained when carers lived at forest houses away from the village. Pigs could forage freely in the forest though they were encouraged to return to the house each evening and were probably usually provided with some fodder. Bananas were seldom available as food - gardens made at a distance from the village had not yielded by the time we departed - but waste and untreated pith from sago palms were available more often than at the village. The pith from 18 palms processed to provide flour was available to 'tended' pigs when they resided with their carers away from the village; i.e. 44 vs 77.5 pig-days per palm when pigs resided at the village. It is likely that additional palms were felled to fodder these pigs.

The management of 'free foraging' pigs was largely invisible to me. Contact was maintained through visits by the primary carer or by a secondary carer who monitored the whereabouts of the pig and reported pending or recent births. Be-

tween December 1986 and November 1987 Gogo visited and remained in the area where two 'free foraging' pigs were under her care on 11 trips totalling 82 days. Similarly, from November 1986 to November 1987, Mabei visited and remained in the area where one pig lived on nine trips (26 days) and Sisigia, who often monitored this pig, visited the area on another 14 trips (39 days). These values exclude day trips to the areas. Activities other than those concerned with pigs were often undertaken during these trips though, in fact, Mabei's 'free foraging' pig was focal to eight of her nine visits.

At least five sago palms were felled as fodder for 'free foraging' pigs and the animals had access to left-overs from at least 15 sago processing ventures (approximately 79 pig-days per palm). Four of the palms were felled during a five month period on behalf of one sow (47 pig-days per palm) and it is probable that the number of palms felled for 'free foraging' pigs greatly exceeded five. At Gwaimasi the pigs classed as 'free foraging' may have been effectively foddered for much of the time though, because the fodder was sago pith, the effort entailed was not great.

By New Guinean standards Gwaimasi pigs were relatively well fed. Estimates suggest that weights in excess of 27.5kg were reached by 60 weeks; at the same age the mean weight of highland pigs from Sinasina, Simbu Province, was 21.6kg (Hide, 1981: 474). Hide remarked that Sinasina pigs grew slowly. All 'free foraging' pigs in the Gwaimasi area exceeded 40kg and two females were 42.5kg and 55kg respectively after birth of their first litters. Hide (1981: 475) reported that sows less than 25kg gave birth in the Sinasina area.

Among Kubo, 'tended' pigs were not released as 'free foragers' until they were about 18 months old and it was only near this age that females attained reproductive maturity (cf. Malynicz, 1970; Hide, 1981: 453).

In October-November 1991, 34 people were classed as residents of Gwaimasi (including one birth and one arrival in the period) and 16 pigs were located in the area. One of these pigs was a five year old barrow. The pigs to people ratio of 0.47 is reduced to 0.40 by including eight people, and one pig, who were formally aligned with Gwaimasi but spent most of their time at Dahamo (Fig. 1) where a primary school was located. Seven of the 16 pigs were 'tended' and one was 'free foraging'. The other eight, owned by members of five families, were in the care of a married couple, who had no children and lived at a fenced tuber garden on the east bank of the Strickland River. In 1986-87 and in 1991 some 'herds' of large pigs, owned by residents of the mission station at Suabi (Fig. 1), were, similarly, in the care of elderly couples without young children, who lived as much as a day's walk from Suabi. 'Swine-herding' of this sort is certainly a recent practice among Kubo. At Gwaimasi, people said they initiated the practice because pigs were spoiling gardens. This assertion sits uncomfortably with an emphasis on growing bananas, which are not attractive to pigs, with the 1986-87 observation that 'free foraging' pigs seldom spoiled gardens and with the lack of concern that wild pigs were a threat to banana gardens. In addition, the people could have fenced gardens or separated 'free foraging' pigs and gardens by the river without the need that some people lived with those pigs. Hyndman (1979: 212) reported that among Wopkaimin 'all pigs (were) kept in residentially separate pig houses ... or in hamlets used solely for pig raising'. As with Kubo in 1991, these animals were in the care of specially appointed community swine-herds (Hyndman, pers. comm.).

DISPOSAL OF PIGS

From August 25, 1986 to November 15, 1987 449.6kg of domestic pork (edible weight) were available for consumption at Gwaimasi (Table 2). This value includes all the meat from seven pigs in the care of Gwaimasi residents, four pigs in the care of non-Gwaimasi residents and 13 piglets, born to Gwaimasi sows, that were killed on the day they were taken from those sows together with portions of two pigs and one piglet that were carried as gifts to Gwaimasi. Forty-seven percent of this meat was consumed by Gwaimasi residents; an average of 25g per adult-equivalent day of residency (28g with Europeans excluded). The remaining 53% was consumed by visitors to Gwaimasi. The yield of edible meat from wild vertebrates was 255g per adult-equivalent day of residency with 56% derived from wild pigs (Europeans excluded; Dwyer & Minnegal, 1991b). Clearly the total contribution of meat from domestic pigs was minor. Nor was the killing of pigs timed to fill lulls in availability of meat from wild vertebrates; much meat from the latter was available at the time of the feast, on the day before 'nuisance' pigs were killed and on the dates of two curing rituals at which 10kg or more of domestic pork was available (see Table 2).

TABLE 2. Disposal and consumption of domestic pigs at Gwaimasi.

Description	Pigs killed (n)	Days pigs killed (n)	Total kg (edible)	Proportion consumed by residents
Payment to spirit medium	1	1	34.13	0.29
Feast	6	1	292.50	0.37
Curing ritual	3	3	36.24	0.61
Management: 'nuisance'	2	1	63.38	0.76
Management: piglets	12	7	17.40	0.86
Received as gifts[2]	3	3	5.95	1.00
Totals	27	14	449.60	0.47

1. Meat was widely and equitably shared by Kubo people. Estimates of the amounts of pork consumed by Gwaimasi residents assume, unless otherwise known (see text), that residents and visitors received shares in proportion to their numbers.
2. Portions of pigs sent as gifts to Gwaimasi; the combined weight of these portions is taken as the total weight.

Of the total edible weight of pork available at Gwaimasi 242.5kg were derived from pigs whose carers were Gwaimasi residents; removal of one pig whose male owner's residency ceased 4.5 months before the pig was killed reduces this value to 206.7kg. The estimate of 210.5kg consumed by Gwaimasi residents is a close fit to these values. However, the proportions of pork contributed and consumed by Gwaimasi residents varied according to the reasons for killing pigs. These reasons are discussed below.

Management considerations (i.e. control of herd size and elimination of 'nuisance' pigs) accounted for the disposal of 11 piglets that were only a few weeks old, one large piglet that for two months had been left with its mother and two sows that, after farrowing, often raided small village gardens. These pigs, all from the local population, contributed 30% of the domestic pork consumed by Gwaimasi residents. Eighty-six percent of the edible weight of the 12 piglets and 76% of that of the 'nuisance' pigs was eaten by residents of Gwaimasi; the latter were killed when the owner of one was visiting and he, with four companions, received a disproportionately large share of the meat.

One small piglet (1.5kg) and two pigs (17 and 40kg) were killed in connection with three curing rituals. The piglet was sacrificed over the heads of two brothers whose lives were endangered by possible contact with spirits; it was cooked and taken from Gwaimasi for consumption by a visiting male who had danced on behalf of the brothers. At both the other curing ceremonies one hind leg, together with portions of liver and entrails, were needed for ritual purposes (Dwyer & Minnegal, 1988). These portions were subsequently disposed of within the resting place of the spirits of the dead (*toi sa*, forbidden place) through a combination of consumption by bachelor males, burning and throwing to crocodile spirits. Residents contributed 38% of the edible weight of these three pigs and consumed 61%; thus, as hosts to curing ceremonies held on behalf of non-residents, they received more pork than they gave.

On the night before one of the curing ceremonies a visiting spirit medium diagnosed the causes of illness of two people; he received a 52.5kg pig in payment. The animal originated from outside Gwaimasi, was killed and cooked at Gwaimasi and portions amounting to about 10kg edible were given to residents by the spirit medium after he and his son had butchered the cooked meat.

Two medium-sized and four large pigs were killed at a feast on January 3, 1987. These six pigs represented 65% of the total edible weight of domestic pork available at Gwaimasi, and provided 52% of the edible pork consumed by Gwaimasi residents. Residents gave more than they received, contributing 51% and consuming 37% of the edible weight available. The feast was planned several months ahead and preparations were underway in late November 1986. Some people referred to the forthcoming event as *kasimes* ('Christmas', but without recognition of the etymology of that word). Visitors from Gugwuasu to the southeast arrived over several days prior to the feast and participated in arrangements. Most residents from Nanega to the west, together with some of their relatives from further afield, made a formal arrival on the evening before the feast. These people had taken several days to slowly lead (and drag!) two large pigs (100 and 120kg) that were to be killed and eaten. This embarrassed the host community which had readied two 'free foraging' pigs, each at 80kg, to feed guests. Two 35kg 'tended' pigs were selected as additions to the intended contribution.

Many of the people who resided at Gwaimasi, Gugwuasu and Nanega in 1986-87 had lived together at a different locality in late 1984. This community had split with the primary division being between what became Nanega and Gwaimasi. Nanega was established as a viable commu-

nity and village before Gwaimasi. The feast of January 3, 1987 is interpreted as an assertion by Gwaimasi residents that they now qualified as an ecologically viable and socially self-sufficient community (Dwyer & Minnegal, 1992a). Further, the feast served to reduce lingering tensions that had underlain earlier fission while, at the same time, revealing elements of intercommunity competition. This last was demonstrated as well when, on the night before the feast, two men who were perceived within their respective communities as Government-appointed 'go-betweens' (*komit*) exchanged gifts. The Gwaimasi man, who was acknowledged as 'the owner of the party', gave one tin of mackerel and a kilogram of rice and 'lost face' when, in return, he received twice the quantity of both food-stuffs.

Small quantities of domestic pork arrived at Gwaimasi as gifts from particular individuals; once, from a married man (or from his wife who had cared for the pig) to an unmarried female in acknowledgement of current restrictions on the consumption of terrestrial game and, again, as part of the distribution of a death-compensation payment to a female relative of the deceased person. Details of the third case are not known. In total these gifts comprised less than three percent of the domestic pork consumed at Gwaimasi.

With the exception of some transfers of small piglets all domestic pig transactions among Kubo were as pork and not as live animals. The primary contexts in which these transactions were made concerned statements of intracommunity solidarity, re-establishment of intercommunity relations, the needs of curing, death-compensation and, very importantly, though not witnessed by me, initiation (cf. Shaw, 1990, on neighbouring Samo). In addition, meat was eaten at feasts held to celebrate the completion of new longhouses and often this was pork. Presumably there were also a variety of situations, beyond the few seen, when small quantities of domestic pork were given by one individual to another.

WOMEN, MEN AND PIGS

Among Kubo the role of males in the day to day management of pigs was minor. Certainly, the perceptions of males were that pigs were the responsibility of women and, at the same time, the needs of pigs should not take precedence over the needs of men. It was women who should ensure that pigs did not raid gardens. On one occasion, when a woman cooked food for her pig before doing so for men who had felled trees at her new garden, a man complained that the work had made him hungry, the woman's priorities were wrong and, after all, the pig had not cut trees!

With women and dogs, men and youths participated in the capture of piglets from sows. At the village, men built secure fences around small yam plots to protect these from pigs (Dwyer & Minnegal, 1990) and it was usually men who felled sago palms used to fodder pigs. Ear clipping and castration were performed by men and they might assist when 'free foraging' pigs, which had come to the village, were returned to the backswamps. Although this last task was not frequent (n = 9 at Gwaimasi) it was arduous because these pigs were not at ease on a lead. The male kin of a carer also contributed by monitoring the whereabouts of 'free foraging' pigs, helping build sleeping platforms at forest houses and, of course, through gardening work that produced food that was fed to pigs.

It was not often, however, that males handled pigs or directly fed them. Only on one day was the role of 'carer' assigned to a male (Table 1) and only once was a man seen to collect stored sago pith to feed a pig. More often a carer's spouse might assist by taking a village-based pig to a nearby tether site and, for several months, a pig of more than 15kg was usually lifted by a man into and out of the house where it was allowed to sleep. Underlying this lack of direct engagement of males with domestic pigs was the relative exclusiveness of the bond between a carer and her pig(s); other people's pigs were difficult for anyone else to handle and at times were dangerous to approach. When a pig charged everyone ran! The most common exception to these observations was evidenced by males, especially youths, who sometimes treated small piglets as women and girls did by petting and cuddling them or, less often, taking them from the arms of a female and running off as though to steal. Youths occasionally carried a piglet in a string bag, either through the village or at departure with the piglet's carer and, once, for about 10 minutes, a 15 year-old youth walked a piglet on its lead around the village domain. His behaviour was that of public display; the transvestism was striking and was reinforced later in the day by an extended period of cross-dressing.

Details of the ownership of pigs are incomplete. Pigs were individually owned by both males and females with early teenagers eligible to be owners. Ownership and caretakership could be coincident and, usually, ownership rights went to the person who captured a piglet from a sow, wild or

domestic. One effect of this latter pattern was to disperse ownership and inhibit opportunities whereby particular owners might increase their holdings. Though, of course, both carers and owners of sows could exert some control over ownership patterns by choosing the participants in piglet capturing ventures. Pigs in the care of a woman were, if not her own, more likely to be - but were not exclusively - those of close kin. The widow Gogo cared for pigs that belonged to a clan brother, an orphaned youth with affinal links and an unrelated male. The eventual fate of some pigs in exchange was decided from the time they were piglets and, thus, long-term commitment to the caring role was itself a component of the perceived value of that exchange (Dwyer & Minnegal, 1992b).

The direct role of Kubo carers was considerable when domestic pigs were killed, butchered and distributed. For several weeks before 'free foraging' pigs were killed they were attended more closely than usual by their carer and, eventually, were brought to the village to be closely watched and regularly fed. At initiation ceremonies the need for attention was reduced by caging the pigs (cf. Shaw, 1990, on Samo). It was a woman, usually the carer, who, at the time of killing, tethered the pig to a stake, calmed it and stood within a metre or two as a man shot it using bow and arrow.

After pigs had been killed, carers moved away as men dragged the carcass to a rack where it would be butchered. Carers were sad but did not grieve openly, though once the widow Gogo sought relief by taking a year-old child from its mother and carrying the infant for 15 minutes or so. (Public grief by females was more evident when a family dog died.) But carers reappeared when men commenced butchery, standing near and sometimes sitting on the rack. They were likely to be the only women in attendance and, in the later phases of butchery when portions were selected for distribution before cooking, often gave forceful instructions to the men (Fig. 3). Carers contributed to the actual distribution of these portions and were sometimes the sole distributors; they also apportioned and distributed entrails, which women had washed, to other women. At this late phase of the precooking butchery and distribution, when most males had

FIG. 3. The woman Kose gives instructions as a pig she cared for is butchered and readied for distribution. A second woman at the butchering rack was a visitor to Gwaimasi who had been primary carer to another pig that was killed on the same occasion.

dispersed, carers might move freely about the rack as they completed a variety of tasks. Women did not contribute to laying the primary oven though some might cook ribs on an open fire for general distribution before that oven was opened. Carers reappeared and observed carefully as men took cooked pork from the oven and they sometimes participated by instruction and action in the apportionment and distribution of this meat after males had carved it.

The participation and rights of carers in the apportioning and actual distribution of pork from domestic pigs were considerable. The almost exclusive bond that existed between carer and pig presumably underlay this. Certainly, the carer was needed at the moment of killing - few other people could have tethered or calmed the pig. However, the extent of female participation varied. It was probably greatest when ownership coincided with caring. It was relatively subdued at more formal events that were attended by many guests or when they, as carers, had come as visitors with their pigs. Again, when two pigs were killed in connection with a curing ceremony that was under the close supervision of a visiting spirit medium, it was he who controlled both carving and distribution after the pork was cooked; there was no contribution from women.

DISCUSSION

This report of Kubo pig husbandry practices is based on detailed observations of a small number of pigs kept by a small number of people. These observations are sufficient, however, to show that Kubo practices were distinctive. They did not fit expectations derived from general and theoretical statements concerning the variety of strategies from New Guinea. In this sense the Kubo case enlarges understanding of the diversity of connections between people and pigs. The primary aim of the following discussion is to locate the Kubo system of pig production and disposal within a comparative frame; to highlight similarities with, and differences from, other New Guinean systems. After brief comparative comment on ratios of pigs to people I discuss (a) the work entailed in maintaining pigs, (b) the importance of domestic pigs to nutrition and (c) connections between pigs and gender roles.

Pig Populations

Ratios of domestic pigs to people vary widely throughout mainland New Guinea (e.g. Feil, 1987: 45; Kelly, 1988: 150). In broad outline these ratios are relatively high (0.60-2.0 or higher) among societies of the Central Highlands and some fringe highland groups that are either structurally and ecologically similar to, or interact often with, the former; low (0.10-0.30) among middle and low altitude societies of the rainforested interior that have little or no contact with the Highlands; and variable (0-1.0) among coastal and near coastal societies.

Geographically, ecologically and socio-culturally Kubo may be best aligned with low and mid-altitude societies such as Bedamuni, Baktaman, Wopkaimin, Miyanmin, Hewa, Sambia and Umeda where ratios of pigs to people are less than 0.30 (Gell, 1975; Hyndman, 1979; Herdt, 1981; Beek, 1987; Kelly, 1988: 150). Indeed, their territory is contiguous with that of Bedamuni to the southeast and within 60km of Baktaman to the northwest. Data from 1986-87 and 1991 reveal that Kubo kept more domestic pigs per person than did any of the other societies within this cluster. The recorded ratios of 0.27-0.54 are intermediate between those of broadly similar societies and those of Highland societies. Relative to these societies, however, Kubo are by no means intermediate according to other criteria (e.g. human population density, agricultural intensification, importance of sweet potato, existence of ceremonial cycles in which pork or live pigs are exchanged, or gender relations) that have been sometimes connected with the relative abundance of domestic pigs.

The comparative data from 1986-87 and 1991 suggest that the size of the Gwaimasi pig population in the earlier period was neither an artefact of circumstances prevailing at that time nor solely attributable to the extraordinary performance of one carer. In 1991 it was Sisigia, with her spouse, who acted as swine-herds and who had, in effect, assumed the earlier role of the widow Gogo (cf. Table 1). Gogo, in 1991, acted as primary carer to only one 'free foraging' pig. Again, in 1986-87, there was no evidence that Kubo people had increased the size of pig herds through recent decades in response to diffuse impacts of modernization. This contrasts with Kuchikura's (1990) report that Faiwol speakers, at 1000m altitude in the Upper Murray Valley, have, through the past decade, increased reliance upon sweet potato and simultaneously increased the size of pig populations.

Pig Management

Throughout the Central Highlands and in some fringe areas the absolute densities of people and

domestic pigs are relatively high. Maintenance of pigs in these areas is reliant upon provisioning the animals with food, particularly sweet potatoes, that has been grown for this specific purpose. Kelly (1988) described these systems of pig production as 'fodder-based'; they are labour intensive systems that may vary according to the relative importance of fodder and forage (cf. A.J. Strathern, 1988: 198).

Fodder-based systems of pig production permit relatively high ratios of pigs to people. But in some areas of New Guinea similarly high ratios may be achieved in a different way. Among Etoro, of the highland fringe, and Elema, of the coastal lowlands, human population densities are comparatively low but the ratios of pigs to people are like those seen in the Highlands (Kelly, 1988). The lack of significant human impact on forest habitats provides opportunities to forage domestic pigs on 'wild' foods. In these societies, therefore, after an initial period in which young pigs receive close attention and much fodder from carers they are released to forage alone. Pigs that are managed in this way become bonded to their carers and, particularly, to their usual foraging areas; this severely limits the possibility that they can be exchanged *live* between individuals or groups. Kelly (1988) described these systems of pig production as 'forage-based'; they require relatively low inputs of labour. Kelly used the Etoro case to challenge earlier theoretical argument that proposed direct causal links between the elaboration of Highland socio-economic systems and increases in the relative abundance of pigs.

In many low and mid-altitude areas of New Guinea human population density is low, forage for pigs is presumably abundant but the ratio of domestic pigs to people is low. Kelly (1988) suggested that societies located in these areas underutilize available forage. Instead, they direct minor surpluses of garden produce (or sago) to a relatively small number of mature pigs that might be either confined in cages (e.g. Keraki) or closely bonded to their carers and the normal residential sites of those carers (e.g. Marind Anim, Miyanmin, Baktaman). While agreeing that the availability of forage is not limiting in these areas I think Kelly de-emphasized the importance of forage to the pigs that *were* kept by societies of the low and mid-altitudes.

Beek (1987: 26) referred to mature Bedamuni pigs that were 'left to roam about in the forest', Barth (1975: 35) commented that 'fully trained' Baktaman pigs 'can be allowed to roam freely', Hyndman (1979: 212-213) reported that Wopkaimin allowed domestic pigs 'to spend a considerable amount of time foraging in the Mid-mountain Rainforest and secondary forest' and Baldwin (1982: 36-37) wrote that pigs kept by the coastal Gogodala 'are provided with only a minimum of food' but, rather, forage on scraps within the village area and 'venture into the nearby bush, where ... they seek out and consume such diverse wild foods as fruits, roots, worms, grubs, as well as reptiles and small mammals'. Although, in all these societies, pigs receive some rations directly from people, and, as with Etoro (Kelly, 1988: 116; Dwyer, 1990: 58), may do so through most of their lives, the impression left by most reports from low and mid-altitude societies is that, as with Etoro and as Morren (1977: 294) wrote of Miyanmin, very little human effort is expended on the production of pigs. Management of pigs by Kubo did not fit this generalization.

Management of pigs by Kubo was, at the least, time-intensive. For 12 to 18 months pigs were in the daily care of women. They were five months old before they spent the day foraging apart from their carers; among other low and mid-altitude societies, and in the Etoro case, this is about the maximum age at which the bond between pig and carer is relaxed by releasing the pig to forage alone or with other pigs. 'Tended' Kubo pigs were routinely provided with fodder, though they foraged as well, and, once released to 'free forage' in the forest, were regularly visited and often provided with pith from sago palms that had been felled on their behalf. I suggested above that 'free foraging' animals were effectively foddered for much of the time. The use of sago as a reliable source of fodder for these animals had the effect that their movements within the forest were likely to be localized and, with both 'tended' and 'free foraging' pigs, may have contributed to the moderately high growth rates inferred earlier. Hughes (1970) summarized experimental data that showed that pigs fed on sago gained more weight than others fed on sweet potato; he noted also that the fibrous pith of *Metroxylon* sago, which is favoured as pig fodder, is rich in protein. Certainly, 'free foraging' pigs were noticeably fatter than the wild pigs killed by Kubo men. Most of the latter were taken in the forested foothills; all of the former had lived in the backswamps.

On a day to day basis the management of pigs by Kubo was not labour intensive. About 6% of banana production was directed to pigs; some of this probably derived from bunches of inferior quality. This is less than Morren's (1977: 294)

estimate of 16.2% of Miyanmin garden produce fed to pigs in the form of undersized tubers and scraps and, of course, much less than the estimates of 30% or more of garden produce directed to pigs among societies of the Highlands (e.g. Rappaport, 1968; Waddell, 1972; Hide, 1981). Again, though Kubo pigs were fed much sago, the labour investment here was small. With 'tended' pigs the on-going tasks were providing (and sometimes cooking) food, attention to hygiene, making tether and lead ropes and, with larger pigs, the retrieval of animals that broke tether and wandered free within the village. Carers had much latitude as regards daytime management: they could 'herd' their pigs, which happened sometimes and had the effect that the woman concerned could do little else at the same time; they could tether the pigs in the forest which meant that the tether sites had to be changed several times in the day; or, as happened most often, they could combine the care of pigs with whatever other activity they had chosen for the day. Again, therefore, it was the investment of time and not of labour that was of primary significance in the management of pigs by Kubo. And the important outcome of this pattern of investment was that the bond established between a pig and its carer was exceptionally strong and, effectively, non-transferable. This bond was more important than bonds to specific foraging areas that might be established through long term familiarization with those areas. Domestic pigs sometimes returned from the forest, or crossed the Strickland River, to find their carers; I have no records of pigs returning to favoured foraging areas (cf. Dornstreich, 1973: 244). This argument has implications concerning patterns of management in areas where human populations are relatively mobile (cf. Hyndman, 1979: 212).

Relative to descriptions of pig management practices among other low and mid-altitude societies of the interior, Kubo practices were similar as regards low investment of labour but differed in terms of the much greater investment of time, the importance of fodder (where this includes sago) and a heightened degree of bonding. Except on one count they differed in the same ways from Etoro. Though Kelly (1988: 119) concluded that Etoro pig-keeping practices 'require minimal labor inputs' he did not refer to the fact that Etoro gardens are fenced and that this task is necessary only because both wild and domestic pigs are strongly attracted to sweet potato. Indeed, at higher altitudes of Etoro territory, wild pigs were rare and all garden fencing (8.27km in 12 months by 109 people; Dwyer, 1990) must be regarded as labour invested in the management of pigs. Thus, among Etoro, the investment of labour in the management of domestic pigs is, in fact, relatively high as, of course, it is among Highlanders who must fence gardens to protect sweet potato[2].

Among Kubo the investment of time in the care of pigs and the bond established between pigs and their carers were correlated. Both may be linked, at least in part, to the fact that Kubo kept many dogs that were life threatening to free-running piglets (Dwyer & Minnegal, 1992b) and to the necessity to isolate the numerically small domestic population of pigs from the very much larger wild population. Kubo pig management practices constructed 'psychological' fences between domestic pigs and their wild counterparts; without this barrier there might have been no 'domestic' pigs. In fact, among Kubo, the 'tended' pigs of one carer were effectively isolated from those of any other carer; this is not the usual state of affairs elsewhere in New Guinea. Taken overall, this discussion of Kubo management procedures suggests that future comparative analyses should attempt to disassociate the variables of fodder vs forage, time vs labour investment, and bonding to carer vs bonding to foraging area. In earlier studies these have been often treated simplistically. Within New Guinea, there are multiple expressions and many possible combinations of these important variables.

Pigs and Nutrition

Pigs feature prominently in proposed explanations of social and agricultural evolution in New Guinea. The central theme of most accounts within this genre is a concern with the emergence and elaboration of Central Highland's formations from precursors in which the social relations

[2]There is a problem for analysts here. When Kubo people fence tuber gardens they state that they are doing so to control pigs; it is easy to categorize the work as connected with the management of pigs. But when Highlanders, and Etoro, initiate gardens by enclosing areas within a fence their perceptions appear to be that the work is integral to gardening despite the fact that there would be no need for that work if there were no pigs. Analyses of the division of labour associated with different subsistence domains might reach different conclusions when making fences is regarded as gardening or as pig management respectively. Conclusions might vary also as the perspective of analysis shifts from 'operational' to 'cognized' in the sense of Rappaport (1968).

within and between groups were different and the production of both garden foods and pigs was less intensive (Morren, 1977; Watson, 1977; Modjeska, 1982; Feil, 1987; Kelly, 1988). These accounts differ from each other in the emphases assigned to ecological and social determinants of the context and process of change, in the connections proposed between pig production and expressions of inequality within social groups and, indeed, in situating gender inequality as relatively early or relatively late in the proposed evolutionary sequences.

One theme, however, appears to unite these interpretations: intensification of pig production within New Guinea is thought to be connected with a decrease in the availability of wild animal protein sources. This connection may be explicit or implicit. It is associated with either the earlier phases of transformation (e.g. Morren, 1977; Watson, 1977; Modjeska, 1982; Feil, 1988; see also Golson, 1982) or thought to emerge later as human and pig populations increased in parallel and the demands of the former led to forest reduction and a need to provide pigs with large amounts of garden produce in lieu of forage (Kelly, 1988). The former view, at least, implies that domestic pigs were an important source of supplementary animal protein even in areas where the ratio of pigs to people was low.

At the most, the average daily contribution of protein from domestic pigs was 3.75g per 'adult' Kubo consumer (i.e. 15% of edible meat with consumption values for children adjusted as in Dwyer & Minnegal, 1991b). This is less than 10% of the protein derived from wild vertebrates. In addition, Kubo ate many invertebrate animals, with crayfish, shrimps (*Macrobrachium*) and weevil larvae adding considerably to the intake of animal protein. Meat from domestic pigs was eaten irregularly and there was no suggestion that domestic animals were killed to fill shortfalls in the supply of meat from wild animals. By New Guinea standards, Kubo ate a lot of animals; their protein intake was probably well in excess of requirements and, hence, the minor contribution from domestic pigs cannot be interpreted as having threshold significance.

I conclude that the production of domestic pigs by Kubo was of no importance in terms of protein nutrition. It is likely that, with few caveats, this conclusion applies throughout New Guinea. It may be the case with some societies that domestic pigs are killed and consumed at times when other sources of protein are scarce or, more likely, that other sources, though available, are foregone at times when domestic pigs are eaten (cf. Morren, 1977: 289). It may be also the case among some Highland societies that protein is generally scarce and the consumption of domestic pigs tips the balance in favour of adequate requirements. But I cannot agree with the statement that for most Highlanders domestic pigs are 'the major source of high-quality protein' (Golson & Gardner, 1990: 396).

The nutritional advantage of animal foods over most plant foods is that the former provide a balanced array of amino acids and, as well, may be the only locally available source of vitamin B12. Some amino acids, often described as the 'essential' amino acids or implicated by statements such as 'complete' or 'high quality' protein, appear to be present in few plant foods. These, together with the more widespread amino acids, must be eaten regularly if human protein nutrition is to be adequate. In New Guinea, pork from domestic pigs is neither eaten in sufficient quantity nor with sufficient regularity to make a significant, on-going contribution to minimal amino acid requirements. Hide (1981: 508) estimated that Waula (Sinasina) people received only 3g protein/person/day from domestic pigs and that, on average, households consumed pork once a fortnight. Through the 12 months of Hide's study the ratio of pigs to people varied between 0.83 and 0.89. Assuming that off-take is proportional to the relative size of local pig populations it is unlikely that the protein contribution from domestic animals approaches 10g/person/day anywhere within New Guinea. Unless it is shown that this is achieved regularly and not, as the literature consistently suggests, very irregularly the conclusion remains unaltered. Norgan et al. (1974) reported high levels of protein intake derived from plant foods among Papua New Guinean Highlanders. Analyses of the amino acid content of New Guinean plant foods are needed to advance understanding of protein nutrition in areas where wild animals seem to contribute little to local diets.

Sorenson (1976: 54) wrote of the Fore that 'sometimes there were periods of several consecutive months without pork, followed by several days of glut after a ceremonial feast'. Occasions of excessive pork consumption are widely reported from Highland societies (e.g. Vayda, 1972: 906). From a nutritional perspective their significance is less likely to concern protein balance than to pose the risk of protein poisoning. Protein foods are potentially toxic unless they are eaten with sufficient quantities of

foods that supply energy (Noli & Avery, 1988; Speth, 1990, 1991). Where protein, from either plants or animals, is used as an energy source then the safe level of intake may fall well below 50% of total calories and, for pregnant females, may be as low as 25% of total calories. Further, high levels of intake of lean meat may be unsafe unless total calories from carbohydrates or fats is increased above normal levels. Noli & Avery (1988: 396), referring to earlier reviews by McGilvery and Speth, wrote that 'when protein is used as the sole source of energy by humans it can lead to nausea and diarrhoea in as little as three days .... It is also clear from the various case study examples cited by Speth that consumption of lean meat alone led to symptoms of starvation and protein poisoning within a week, diarrhoea within 7-10 days, severe debilitation within 12 days and the possibility of death within weeks'. We were reprimanded often by Kubo when we did not cook sago to accompany meals of pork; the people were not convinced that rice was a sufficient substitute for sago.

Carbohydrate foods and fats provide energy in the diet. New Guineans often reduce carbohydrate intake when pork is available in quantity but they may offset the risk of protein poisoning because they prefer, and in many societies deliberately promote, fat pigs. The thought of fat pigs was keenly anticipated by Kubo. A month before the feast one man exclaimed *'Sori! O wai safei kau'* ('Sorry! The fat of domestic pigs is abundant'). The ethnographic literature from New Guinea abounds with reports of similar statements. Baktaman rub pigs with special white, powdered earth to magically promote fat (Barth, 1975: 35), the ideal Keraki pig was one that grew so fat it could not stand (Williams, 1936: 18), Sanio Hewa castrated all domesticated male pigs 'at a few months of age "to make them lie around and get fat"' (Townsend, 1969: 49) and, for the same reason, Marind Anim kept only barrows (van Baal, 1966: 406). In the Highlands people may prevent sows from breeding or increase the supply of food to pigs as deliberate attempts to fatten animals in readiness for killing (e.g. Hide, 1981). Comparable statements or procedures that extol the value of the *meat* of domestic pigs are very rare.

Throughout New Guinea, whether the ratio of domestic pigs to people is high or low, the significance of the animals is located in the social and not the nutritional sphere. If there are, as well, nutritional benefits then these concern fat more than they concern protein. In the first place, fat pigs reduce the risk of protein poisoning, especially on occasions when much pork is eaten and the normal intake of carbohydrate foods is reduced. Here, the nutritional role of fat is indirect - it is a source of energy that reduces risks associated with eating large amounts of meat. In addition, however, early nutritional surveys within New Guinea consistently reported that fat (including lipids) was poorly represented in local diets (e.g. Oomen, 1971). On this count, therefore, the nutritional significance of the fat from domestic pigs may be also, at some times and in some places, direct.

Pigs and Gender

Conventional wisdom has it that among Highland societies inequalities among men and between men and women are intimately tied to patterns of pig production (e.g. Modjeska, 1982; A.J. Strathern, 1982; but contrast with Kelly, 1988). Men strive for prestige. They do so by publicly exchanging valuables, especially pigs and pork. But the labour and time required to rear those pigs has been, for the most part, invested by women. Thus, in pursuit of prestige and leadership, men compete with one another, appropriating the labour of women to their own ends in the process. The outcome is that relations of inequality emerge among males, and women are disenfranchised and disempowered. Under the standard argument these inequalities between individuals and sexes are likely to be greatest where the ratio of domestic pigs to people is highest (cf. Feil, 1987). Indeed, a poignant focus of Highland exchange systems is that, ultimately, the labour invested by women in the production of pigs becomes the means whereby men acquire other women as brides in exchange for those pigs[3].

Among Kubo, relations between men and women were characteristically relaxed and warm. There was no ethos of sexual antagonism and little concern with sexual pollution (cf. Sørum, 1984, on Bedamuni). Public expressions of affec-

[3]In contrast to the standard argument, Feil (1987: 57-58) asserted that gender inequalities were least severe among societies of the Western Highlands where ratios of pigs to people were particularly high and agricultural production was intensive. He thought that 'it is in societies where production and exchange are truncated and circumscribed ... that inequalities, especially between men and women in the production process are the most severe'. M. Strathern (1988) provides a challenging counter to Feil's understanding of gender relations in the Western Highlands.

tion between husband and wife were relatively common (e.g. holding hands, resting in the lap of one's spouse, play-fighting). Aggressive fights were very rare and, for husbands in particular, triggered self-recrimination and a lengthy period of awkward reconciliation. In the subsistence domain, gender roles were conventional and complementary rather than culturally legislated and they were often transgressed. Women sometimes hunted, men sometimes pounded the pith of sago palms and young girls could play with bows and arrows. Though men and women slept in different sections of the communal longhouse, women were not prohibited from entering the men's section. At family houses in the village, gardens or forest there was even less spatial separation between husband and wife.

Kubo women participated less than men in ritual life. They did not dress up and dance as men did (Dwyer & Minnegal, 1988) and, with the possible exception of a focal individual, they (and their pigs) were excluded from seances and the closing moments of curing ceremonies; here, however, the perceived danger was not so much to the women themselves as to infants, including the unborn, with whom women closely associated. But women performed as lead singers and as chorus on all occasions when men danced and, though young women were not initiated, both older men and older women acted as formal sponsors to male initiates. (Among neighbouring Samo, young women were also initiated; Shaw, 1990.)

By New Guinean standards the extent to which female carers of domestic pigs were necessary and active participants when the animals were killed, butchered and distributed was unusual. In ideal circumstances affinal exchanges of pork entailed the simultaneous distribution of meat from two pigs, one contributed by each of the participating groups. This paralleled the ideal of immediate sister exchange as the basis of Kubo marriages. With both the marriages and the exchanges of pork either of the focal women - a bride-to-be or a pig's carer - could veto the intended arrangements. Again, the ideal of simultaneity might not be met because one of the intended partners was judged to be too young or one pig was judged to be too small.

The control that Kubo women exercised over the disposal of domestic pigs may be linked to management practices. The ratio of pigs to people was unexpectedly high and the time devoted to rearing the pigs was considerable. Nearly all the work was done by women and the strategies of management were such that domestic pigs were so closely bonded to particular carers that the animals were non-transferable. (It seems unlikely that this statement will remain true in the new circumstance of communal swine- herding that is being developed by Kubo.) The permission and physical presence of a pig's carer was perceived as essential when the pig was killed. Though carers were not necessarily owners their engagement with a particular pig persisted through the life of that pig. Because pigs in the care of one woman were effectively alienated from association with other people, and from the pigs owned by those people, there was little opportunity for men to usurp the role of women as the time approached to kill the pigs.

Among Etoro it was the person who completed a process of production who controlled distribution of the product (Kelly, ms.); with domestic pigs it was men who retrieved the animals that were to be killed, who killed and butchered them and who distributed pork at events where other men were the public recipients of the gifts (see also Dwyer, 1990: 130-132). By contrast, among Kubo, women prepared the pigs for dispatch, stood with them as they were killed and officiated at distributions. Their participation was greater and more overt than that described for Baruya women by Godelier (1986: 15-16). From the perspective advanced by Kelly the role of Kubo women is understandable; they were needed to complete the process of production and, hence, shared in the process of distribution. But was that role necessary?

It is difficult to assign either ecological or social imperative to the patterns of pig production and disposal described here for Kubo. There were more pigs than expected and, by comparison with ecologically similar societies, it appears that they could have been managed with far less commitment from carers and with far more latitude for dispersing the caring role. Domestic pigs do not need to be dangerous to people who are not their primary carers! The importance of the animals was not to nutrition but, rather, to the satisfaction of a variety of social concerns. At these events the role and status of women may have been less pronounced if management strategies had been different. The simple conclusion is that Kubo patterns of pig production empowered women and contributed to the markedly egalitarian ethos of Kubo society. This conclusion may seem analogous to that of Feil (1987) regarding Tombema-Enga of the Central Highlands; the analogy, however, would be superficial because any similarities arise within social and ecological contexts that

are entirely different. Both Kubo and Tombema-Enga represent distinct transformations of the commonalties that underlie and unite Melanesian social life (cf. M. Strathern, 1988).

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TWO CAVES

BRUNO DAVID AND LIAM DAGG

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This paper presents results obtained from two archaeological excavations undertaken in the Mitchell-Palmer limestone belt, north Queensland. The sites were excavated in order to investigate temporal patterning in the archaeological record, and especially to obtain information on the antiquity of rock art in the region. In line with previous models of change in Aboriginal prehistory, the results indicate major changes during the mid to late Holocene. They also indicate that the rock paintings from the region may largely date to the last 3500 years, whereas the peckings may be older. □ *Australian prehistory, rock art, north Queensland, intensification, cave paintings, rock engravings.*

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In 1983, Lourandos argued that, in many parts of Australia, major social and cultural changes took place during the mid to late Holocene. Amongst other things, archaeological evidence for these changes include significant increases in deposition rates of cultural materials within individual sites, increases in the number of occupied sites in the landscape, a broadening of resource exploitation strategies (including diet breadth), and major changes in stone artefact technologies. Together, it has often been suggested that these points implied major increases in intensities of site and regional land use (e.g. Hughes & Lampert, 1982). What has been lacking, however, is data to determine the relationship of the separate regional sequences, so as to enable an investigation of the dynamics of structural phenomena, such as inter-regional relations, alliance systems and exchange networks. It is these issues, it is argued, that would enable us to better understand the social contexts of the archaeological changes documented so far.

This paper emanates from these concerns. It presents the results of two archaeological excavations undertaken in the Mitchell-Palmer limestone belt, north Queensland, forming part of a broader research program focusing on the dynamics of socio-cultural (inter-regional) relations during prehistory. In order to investigate socio-cultural structure in prehistory, rock art has been the object of enquiry. Rock art is treated as governed by socio-cultural conventions, so that by investigating continuities and discontinuities in the distribution of rock art through space and time, socio-cultural patterning is itself being investigated. To shed light on such patterns, a number of sub-regions within north Queensland have been systematically surveyed for rock art sites, thereby enabling an investigation of spatio-temporal trends in rock art conventions.

This paper is a contribution towards these investigations. In order to determine the antiquity of the art, a number of rock art sites were excavated. These excavations enabled the recovery of in situ pieces of pigment (the by-products of artistic endeavours), as well as information on other temporal trends (e.g. stone artefact deposition rates). Together, these data have contributed significantly to our understanding of change and stability in the region.

The aims of this paper are thus to report on excavations undertaken at Hearth Cave and Mordor Cave. In presenting the data obtained from these excavations, broad trends will be revealed, trends that are consistent with those obtained from other sites in north Queensland (David, in prep.).

THE MITCHELL-PALMER LIMESTONE BELT

The Mitchell-Palmer limestone belt consists of a 60km long and 5km wide belt of karst towers (Fig. 1). Caves are abundant throughout the limestone (Fig. 2), two of which were excavated by the author in 1989 (Mitchell River Cave and Hearth Cave). Mordor Cave, located in the Mordor North Tower, was excavated by one of us (BD) in 1991. In all cases, excavation followed the Johnson (1979) method of bucket-spits. All

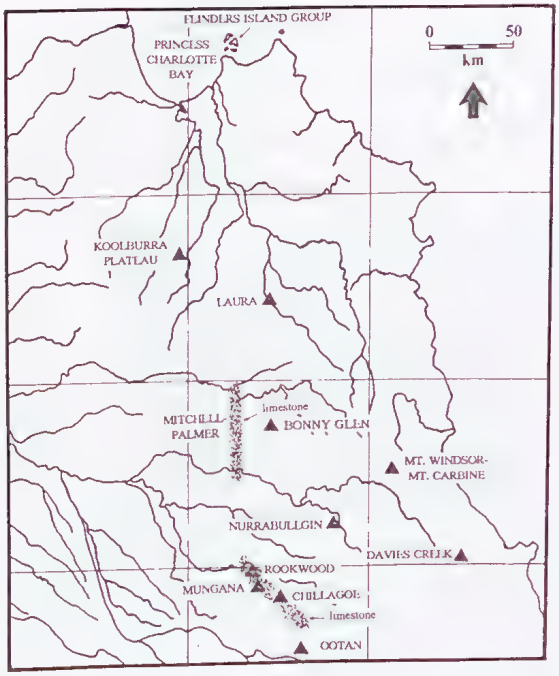

FIG. 1. Southeast Cape York Peninsula, showing location of the Mitchell-Palmer limestone belt in relation to other areas where rock art has been recorded. Arrow points to magnetic north.

cultural materials 2cm maximum size were plotted in three dimensions, and all other materials were sieved in 3mm-mesh sieves. As the results from Mitchell River Cave have already been presented elsewhere (David, 1991a), this paper only documents the Mordor Cave and Hearth Cave data.

TABLE 1. Number of paintings and stencils, Mordor Cave.

FIGURATIVE PAINTINGS		
Anthropomorphs:	vertical	204
	diagonal	8
	upside-down	6
	horizontal	2
		30
Bats		11
Dog		3
Boomerang		1
Pig		1
Crocodile		
TRACK PAINTINGS		
Bird		4
NON-FIGURATIVE PAINTINGS		
Geometric		22
Other linear		4
Grid		2
Infilled area		2
STENCILS		
Hand		10
Boomerang		1

MORDOR CAVE

Mordor Cave is a large limestone cave with an uneven, rocky floor located 12 km north of the Mitchell River. It was first rediscovered by L. Pearson on the 17 June 1979, when the Chillagoe Caving Club undertook speleological explorations in the Mitchell-Palmer limestone belt. Mordor Cave was described by the Chillagoe Caving Club Inc. (1988: 43) as having

> 'three large entrances interconnected with twilight and dark zones linking them horizontally. A peripheral system with some excellent decoration. Aboriginal paintings are executed on walls in mono- and bichrome silhouettes. There are over 140 individual paintings of human figures, dingoes, emus, bats and crocodiles. A pool of water would have served for ochre preparation. Some hand stencils and some inverted figures.'

The main entrance to the cave involves a moderate climb up boulder-strewn pediments, followed by a descent onto a flat floor located near the back wall. It is here that the only occurrence of soft, ashy deposits is located (Fig. 5). On the cave wall are 300 paintings and 11 stencils, most of which are monochrome infilled and red in colour (Table 1, Figs 3, 4). A number of roof collapses give entry to deep caverns along both ends of the cave. Two edge-ground axes and a stone flake were found amongst collapsed material which can be reached by a short walk through pitch-black corridors in these caverns. It is possible, however, that the artefacts were thrown into the collapsed chambers from the skylit chamber above (that is, the main chamber containing the soft ashy deposits).

Mordor Cave was excavated mainly because of

FIG. 2. Limestone karst tower, Mitchell-Palmer limestone belt.

FIG. 3. Mordor Cave, painting of a pig.

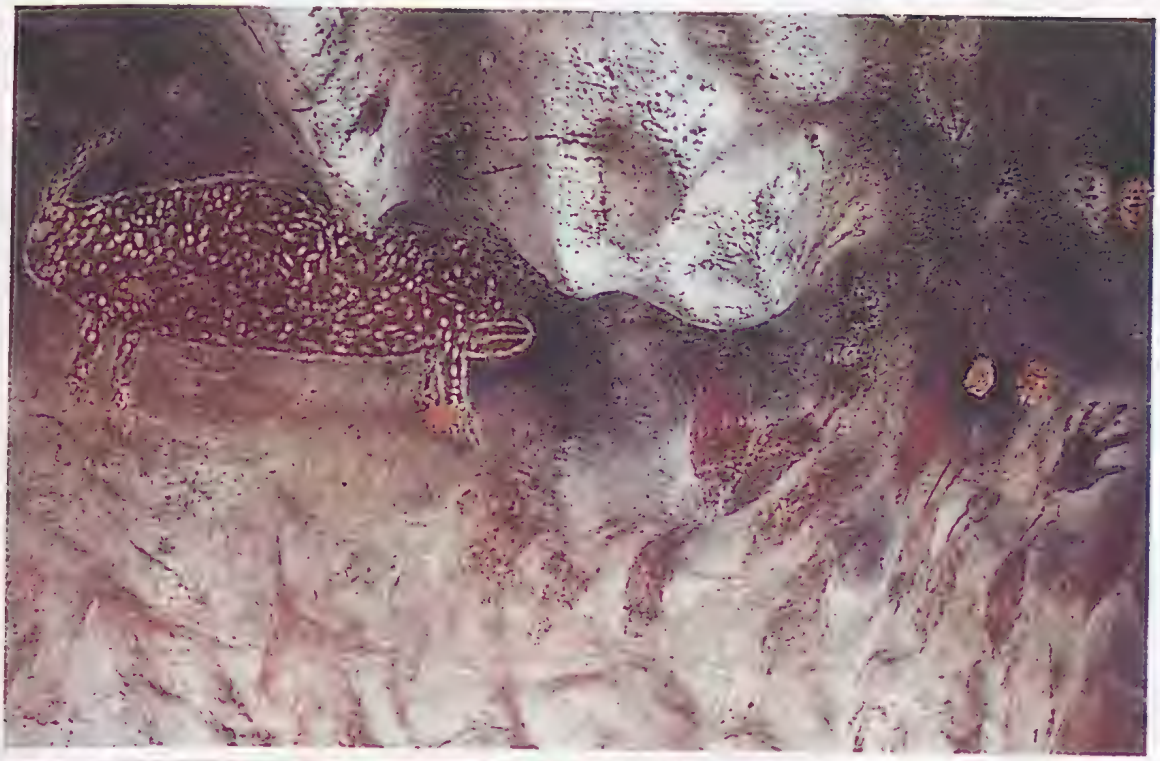

FIG. 4. Mordor Cave, main painted panel.

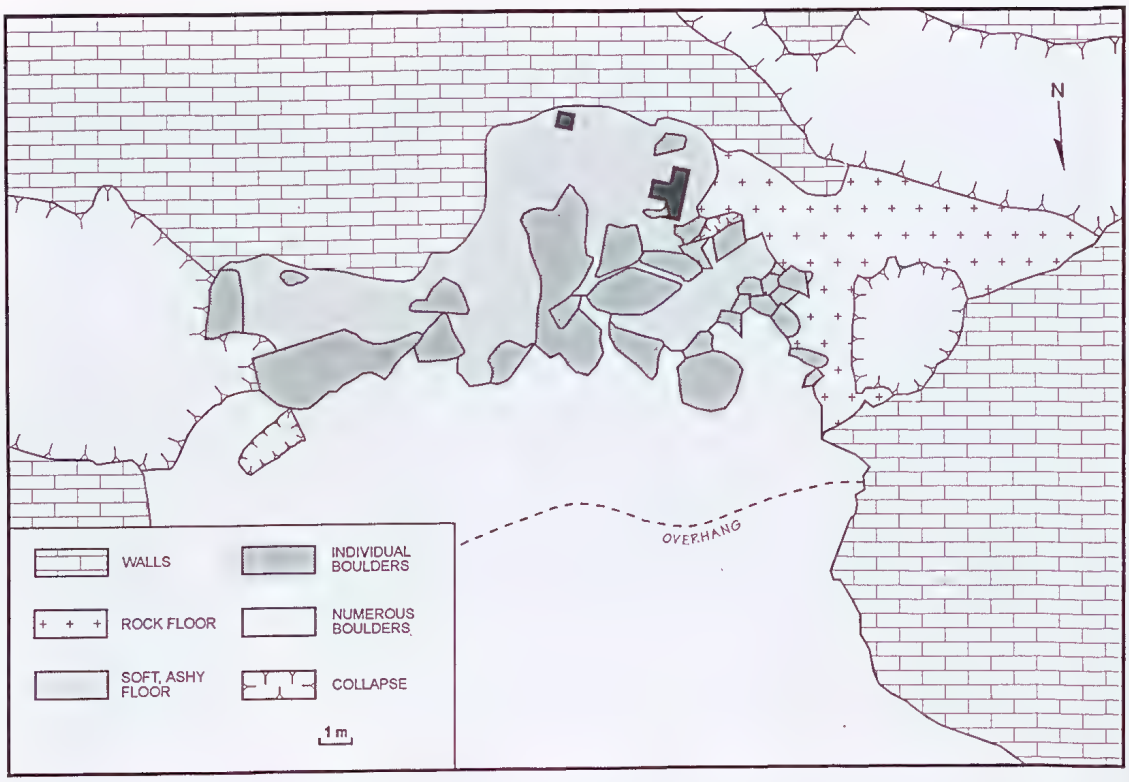

FIG. 5. Mordor Cave, site plan. The arrow points to magnetic north. The excavation squares are represented in infill; Square E18 is the isolated square, and H10 is the centre square of the T-shape excavation.

the large numbers of paintings and stencils on the cave wall, immediately adjacent to soft archaeological deposits. The great numbers of paintings located within a spatially constricted area near soft deposits were deemed to offer great potential for the recovery of in situ ochres, offering the possibility for dating the art by association with dated, in situ ochres. Two test excavations were undertaken in the soft ashy deposits. Square E18 consists of a single 50cm× 50cm pit located near the centre of the soft deposits, where sediments appear to be at their deepest in this part of the site. The main excavation was undertaken 3.5m from square E18, and consists of squares G10, H10, H11 and I10. Square H10 was initially chosen for excavation because it was located in what appeared to be the deepest part of the site. Squares E18, G10 and H10 were excavated to bedrock, while squares H11 and I10 were only partly excavated in order to enable access into adjacent squares G10 and H10. In total, 1.25m^2, or 2.0% of the 66m^2 of soft ashy floor, were excavated. All excavated sediments were very dry at the time of excavation. At some distance from the ashy deposits, closer to the dripline, large lag deposits indicate the existence of drip points and seasonal pools of water.

The excavated materials from squares E18 and H10 have been sorted and analysed and are presented here.

TABLE 2. Stratigraphic Units (SUs) from Mordor Cave, square E18.

SU	pH	Dry	Munsell	Description
1	8.5	10YR	6/2	Surface sediments, grey in colour and ashy in composition. It is loose and appears to be very disturbed. No vegetation appears on the surface.
2	8.5	10YR	6/2	Ashy sediments whose texture is similar to SU1, but with a moderate compaction. Sediments show no evidence of disturbance. No internal stratification is evident.
3a	8.5	2.5YR	3/2	Very dark, black, charcoal-rich sediments with patches of white ash
3b	7.5	10YR	5/4	Brown silty deposits with a high charcoal content. Very rich in vegetation. Vegetation appears horizontally bedded immediately above the bedrock.

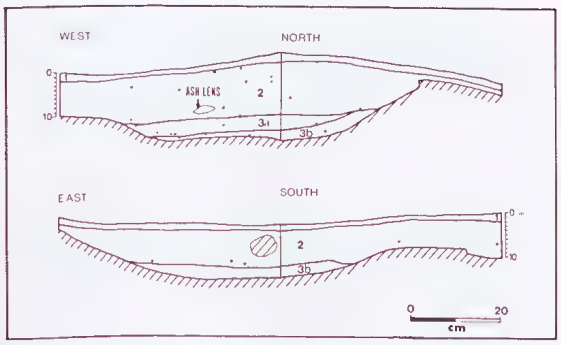

FIG. 6. Mordor Cave, Square E18 stratigraphy. The dots represent pieces of charcoal.

Square E18

Square E18 is well stratified, containing three Stratigraphic Units (SUs), SU3 being further subdivided into two sub-layers (Table 2 & Fig. 6). All stratigraphic units are well defined. Excavation proceeded in seven Excavation Units (XUs), the average thickness of which was 2.6cm.

Square E18 is 20.0cm deep. A single radiocarbon date was submitted from XU7, immediately above bedrock. A radiocarbon date of 1640±70 BP (Beta-46090) was obtained, with a $\partial^{13}C$ value of -28.4‰. The $\partial^{13}C$-adjusted age of 1580±70BP is taken to date the beginnings of occupation in this part of the site.

Table 3 presents a complete list of materials recovered from E18. The fauna is listed in Table 4. In Table 5, the raw data have been converted to deposition rates per m^2 per centimetre of deposit, to enable comparisons of deposited materials by XU. Because only a single date was obtained from square E18, the time frames covered by each spit could not be calculated. Therefore, deposition 'rates' were obtained by calculating the amounts of material recovered per m^2 per centimetre of deposit. These deposition 'rates' are graphed in Fig. 7.

SU1, represented by XU1, contains relatively low amounts of charcoal, bone, land snails, stone artefacts, eggshell, mussel shell and ochre. The proportion of burnt eggshell is also low. Compared with underlying SU2, the sediments contain large amounts of organic material (especially twigs and bark), and compaction is relatively low (as measured by weight per volume). These findings are not surprising given that, firstly, the site is not believed to have been occupied during the last 100 years, and secondly, that the surface sediments were very loose during excavation.

SU2, represented by XUs 2-5, contains large numbers of stone artefacts, land snails, eggshell, mussel shell, ochre, charcoal and burnt earth. Quantities of all cultural materials are relatively low towards the lower boundary of SU2. This may indicate that a hiatus is represented at the SU3-SU2 boundary, or that XU5, the lowermost XU from SU2, should be treated as an interface between SU3 and SU2. This interface should be treated as comprising of intermixed SU3 and SU2 materials.

SU2 contains relatively compact sediments and relatively low amounts of organic materials (mainly vegetation), except for XU5. Here, the organic content is similar to that from underlying SU3a. This further re-enforces the likelihood that XU5 contains materials from the underlying stratum.

SU3a is represented by XU6. It is rich in stone artefacts and bone, but relatively poor in all other cultural materials. Sediments are very compact

TABLE 3. List of materials excavated from Mordor Cave, Square E18.

XU	SU	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	1	395	6.5	7.0	127.5	264.3	1.9	3.9	0.25	2.8	76.1	33.3	30	5.9		0.20	1.6	7		0.6	56	8.5	670	4	
2	2	276	4.5	5.0	164.7	131.7	2.2	1.8	0.25	2.9	25.5	20.6	10	2.8	1	0.28				0.2	8	5.6	348		
3	2	675	6.3	6.0	358.4	100.0	4.3	2.1	0.24	2.9	69.3	16.8	23	58.0		2.52	1.1		1	0.2	28	9.9	648	4	1.1
4	2	216	5.3	5.0	324.9	129.9	1.4	2.8	0.23	9.5	48.5	31.8	10	13.7		1.37	21.9	1		0.2	20	6.0	412		
5	2	313	5.0	5.0	190.8	231.4	1.2	2.3	0.22	1.7	22.4	29.0	19	12.9		0.68	1.3	1		0.3	21	2.9	198		78.6
6	3a	208	5.3	3.5	111.1	160.7	0.8	2.4	0.18	0.3	14.6	28.6	37	27.2		0.74				0.5	42	0 6	59		
7	3b	37	0.8	1.0	67.7	53.2	0.2	2.9	0.13		4.1	4.5	27	8.8		0.33				0.1	2	0.1	3	1	

1=residue >3mm (g); 2=sediments excavated (kg); 3=sediments excavated (litres); 4=charcoal (g); 5=other organics (g); 6=land snail (g); 7=mean thickness of XU (cm); 8=area excavated (m^2); 9=mussel shell (g); 10=burnt earth (g); 11=bone (g); 12=flaked stone artefacts (#); 13=flaked stone artefacts (g) 14=fungus (#); 15=mean weight of flaked stone artefact (g); 16=ochre (g); 17=ochre showing no use-wear (#) (all are red); 18=ochre showing use-wear (#) (red); 19=burnt egg shell (g); 20=burnt egg shell (#); 21=unburnt egg shell (g); 22=unburnt egg shell (#); 23=seeds (#); 24=burnt stone (g).

TABLE 4. Mordor Cave faunal remains: Minimum Numbers of Individuals (MNI), Square E18 (after Dagg, 1992). Question marks indicate the presence of identified species which are believed to be post-depositional intrusions into that unit (for reasons outlined in Dagg, 1992). P=present.

Species	SU1	SU2	SU3a	SU3b	Total
Macropus agilis	1	1	?	0	2
Petrogale sp.	1	2	2	?	5
Trichosurus vulpecula	1	?	1	?	2
Peramelidae	1	1	?	0	2
Macropus gigas	0	1	0	0	1
Uramys caudimaculatus	1	2	0	1	4
Other Muridae	3	9	1	1	14
Canis familiaris	0	1	0	0	1
Agamidae	0	1	0	0	1
Scincidae	0	4	0	0	4
Boidae	0	1	0	0	1
Teleostomi	3	3	1	0	7
Velesunio sp.	P	P	P	P	
Xanthomelon sp.	P	P	P	P	
Alectura lathami egg	P	P	P	P	

and contain very high amounts of vegetation. The percentage of burnt eggshell is very high.

SU3b (XU7) contains low amounts of all cultural materials except for stone flakes. Sediments are not as compact as overlying SU3a, and their organic content is low. The percentage of burnt eggshell is very high.

The part of Mordor Cave represented by Square 18 is interpreted as having been first occupied approximately 1500 years ago. At that time, occupational intensities were low. During SU3a times, large amounts of organic material, including bark and twigs, were laid horizontally on the cave floor. This layer is well defined, and associated with a low deposition 'rate' of all cultural materials, except for stone artefacts and bone. Stone artefacts are very small, averaging 0.7g. These factors indicate that the sediments recovered from SU3a may have been a sleeping mat, and that during this time the area was used as a sleeping area. It is therefore possible that contemporaneous materials from other parts of the cave would reveal complementary, specialised activity areas, such as hearths and stone artefact manufacturing areas.

During SU2 times, Square E18 witnessed relatively intensive deposition of cultural materials. It is during this time that most of the paintings on the walls were probably undertaken, as indicated by peak ochre deposition rates during this time. Fires lit during SU2 times may have caused the high proportions of burnt eggshell in XU6 and XU7 underneath. As eggs cannot be roasted directly on a fire (or they would shatter or explode; L. Hughes, pers. comm., 1992), burnt fragments of eggshell are likely to represent subsequent burning by overlying hearths.

The well preserved sediments also contain one large bracket fungus (Fig. 8). It is a single sporocarp of a member of the order Aphyllopharoles, family Polyporaceae. It is probably from the genus *Polyporus*, and possibly *P. udus* (P. Bostock & C Young, pers. comm., 1992). The dryness of the cave, and the compaction of the sediments, indicate that it could not have grown in the deposits, but must have been introduced into the cave. Such fungi are known to have been eaten by Aborigines in north Queensland during ethnographic times.

SU1 times include the post-contact period, including the recent period when the site was abandoned. Consequently, the low densities of cultural materials during this time are not surprising.

Square H10

Square H10 is 114.5cm deep, containing four distinct Stratigraphic Units, some of which are further sub-divided into a number of sub-units (Fig. 9). The SUs are described in Table 6.

TABLE 5. Mordor Cave, Square E18: deposition rates (per m^2 per cm of deposit), and proportions of burnt eggshell.

XU	SU	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	1	6.7	6.1	1.95	130.8	78.1	30.8	6.1		7.2	1.6	2.9		271.1	744.6	9.3	6.6	4.1	34.2
2	2	10.0	5.8	4.89	366.0	56.7	22.2	6.2				6.4	2.2	292.6	791.1	12.9	3.4		45.8
3	2	12.5	9.7	8.53	711.1	137.5	45.6	115.1	2.2	2.0	2.2	5.8		198.4	1341.3	20.0	2.0	7.9	33.3
4	2	8.3	3.9	2.17	504.5	75.3	15.5	21.3		1.6	34.0	14.8		201.7	670.8	9.6	4.6		49.4
5	2	9.9	5.9	2.37	377.1	44.3	37.5	25.5	155.3	2.0	2.6	3.4		457.3	235.2	6.3	9.4		57.3
6	3a	12.3	3.8	1.85	257.2	33.8	85.6	63.0				0.7		372.0	233.8	2.6	45.5		66.2
7	3b	2.1	4.4	0.53	179.6	10.9	71.6	23.3						141.1	13.3	0.5	50.0	2.7	11.9

1=sediments excavated (kg); 2=% residue >3mm; 3=land snail (g); 4=charcoal (g); 5=burnt earth (g); 6=flaked artefacts (#); 7=flaked artefacts (g); 8=burnt stone (g); 9=ochre (#); 10=ochre (g); 11=mussel shell (g); 12=fungus (#); 13=other organics (g); 14=egg shell (#); 15=egg shell (g); 16=% egg shell burnt (by weight); 17=seeds (#); 18=bone (g).

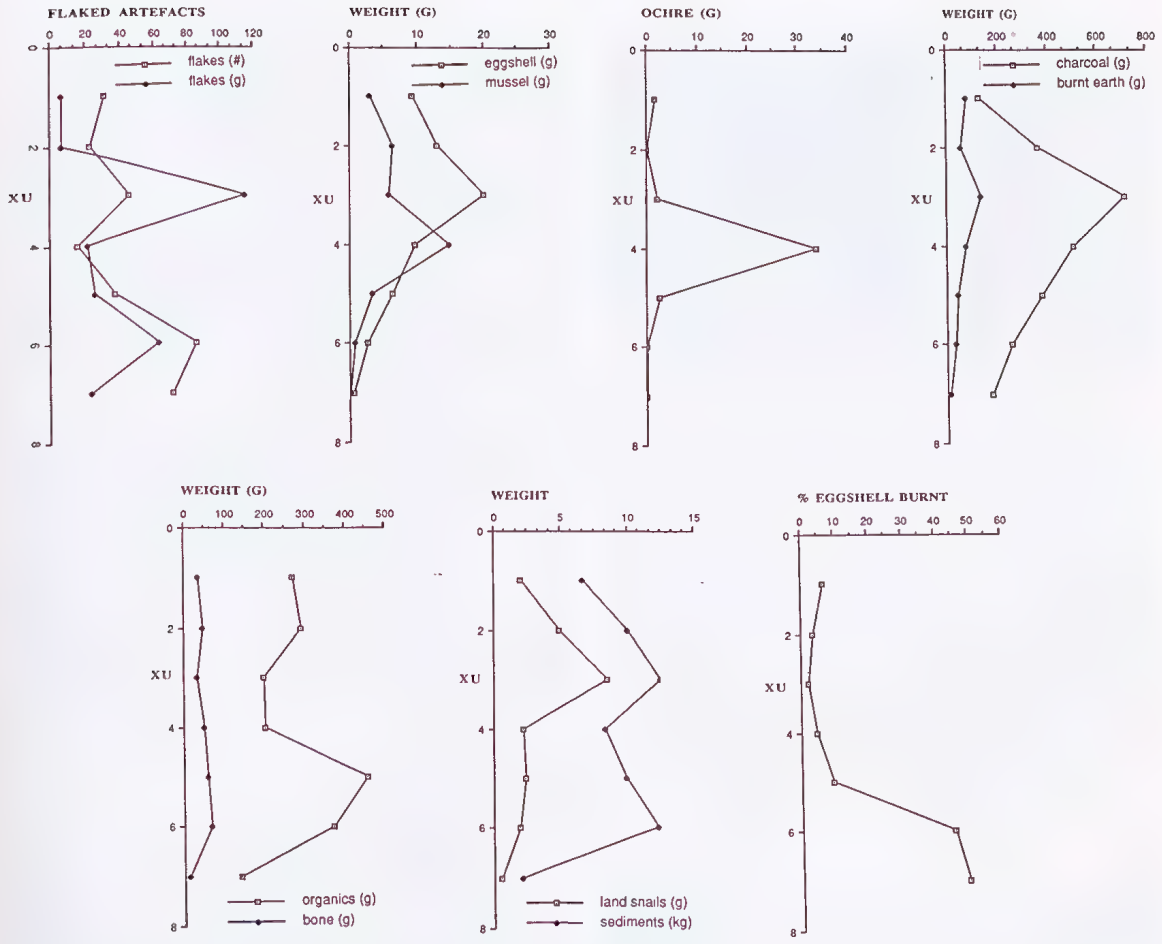

FIG. 7. Mordor Cave, Square E18, deposition rates (per m^2/cm of deposit) and proportions of burnt eggshell.

Two radiocarbon dates were obtained from Square H10 : 980±60BP (Beta-46317), located 84.7cm below the ground surface, in XU25 (SU4). The $\partial^{13}C$ value equals -27.6‰, and the ^{13}C-adjusted age is 940±60BP; and 850±50BP (Beta-46318), located 114.0cm below the ground surface in XU28 (SU4). The $\partial^{13}C$ value equals -28.2‰, and the ^{13}C-adjusted age is 800±50BP.

The two radiocarbon dates are similar and overlap at two standard deviations. They are taken to confirm the impression gained during excavation, that SU4 is an archaeologically instantaneous event.

Square H10 was excavated in 28 spits, XU10 of which was excavated in three sections (XUs 10a, b & c). Table 7 documents the amounts of materials excavated from square H10. Table 8 presents the deposition 'rates' as calculated per m^2 per centimetre of deposit (Fig. 10), while Table 9 lists the fauna identified from square H10.

SU1: this unit consists of XU1 and XU2. It contains relatively large amounts of charcoal, burnt earth, stone artefacts, mussel shell, eggshell, seeds and other vegetation. In short, SU1 represents a peak in deposition rates of a number of cultural materials.

SU3: this unit consists of XUs 3-6. It contains varying but relatively low amounts of cultural materials. XU7 is an interface between SU3 and SU4.

SU4: this unit consists of XUs 8-28. The lowermost seven XUs (23-28) are from SU4h, which appears to be a localised variant of SU4, containing leaves and seeds amongst a rich vegetation (especially bark and twig) matrix. Leaves do not occur above XU22. Whilst SU4 contains similar amounts of cultural materials to SU3, SU4h contains significantly higher amounts of bone and a greater proportion of burnt eggshells, with ochre and pandanus nuts occurring exclusively in this

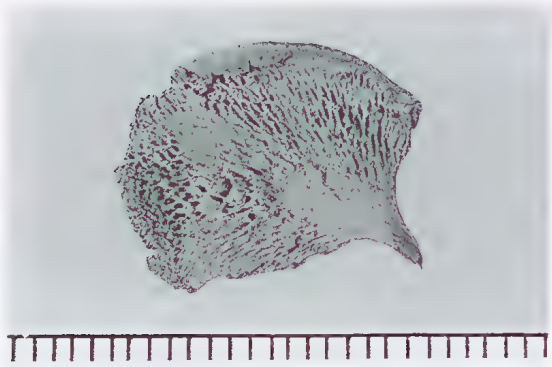

FIG. 8. Bracket fungus found in XU2, Square E18, Mordor Cave (scale in 2mm units).

unit. Amounts of charcoal are more variable between XUs of SU4h than is the case in SU4 proper above it. SU4h sediments contain a relatively high proportion of sediments over 3mm in minimum size, although stone artefacts are very rare. Interestingly, XUs 20-21, located near the boundary of SU4 and SU4h, contain 98.2% of the burnt stone recovered from Square H10. Given that relatively high percentages of burnt eggshell, as well as consistently high amounts of charcoal and burnt earth also appear in this part of the excavation, SU4 and SU4h may be related to a hearth. This is also supported by the fact that some of the vegetation making up the organics from SU4 is partly burnt. SU4 and SU4h may therefore represent materials dumped when a cooking hearth was emptied to retrieve the cooked food. However, while this explanation would explain the 'instantaneous' appearance of the deposits and the burnt material, it does not account for many of the cultural remains within SU4/4h (see below).

A number of wooden objects, including a digging stick (from XU22) and a large sheet of cut bark containing a number of pandanus nuts around and on top of it (XU25), were also located within SU4 (Fig. 11). A grinding stone with two ground surfaces was also recovered from XU 26. All of the ochre (3 white pieces, totalling 1.4g), none of which contained use-striations, came from XU25 and XU27. A fig (*Ficus virens* var *sublanceolata*, *F. obliqua*, *F. platypoda*, *F.*

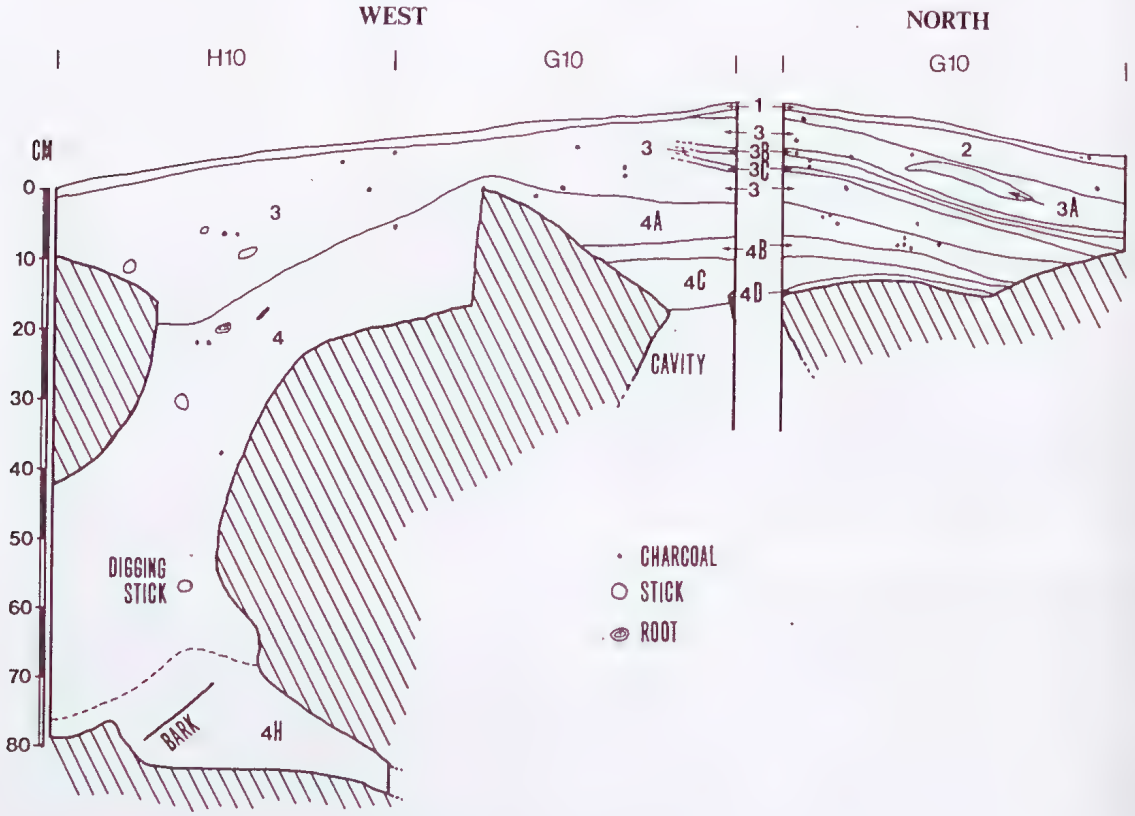

FIG. 9. Mordor Cave, Square H10 stratigraphy.

TABLE 6. Stratigraphic Units (SUs) from Mordor Cave, square E18.

SU	Dry	Munsell	Description
1	10YR	6/2	Loose, disturbed, grey, asy.
2	10YR	6/2	Some vegetation present especially in some parts of Square G10. Brownish-grey in colour. Ashy and moderately compact.
3	10YR	6/2	Ashy, grey
3a	10YR	6/2	Localised lens of vegetation.
3b	10YR	6/3	Well-defined, fairly compact.
3c	10YR	6/3	Well-defined, fairly compact.
4	10YR	5/3	Very rich in vegetation. This unit contains very little sediment apart for the matted vegetation.
4a	10YR	6/3	Dark grey vegetation sub-layers.
4b	10YR	5/3	A grey vegetation sub-layer.
4c	10YR	6/3	Dark grey vegetation sub-layers.
4d	10YR	3/1	A grey vegetation sub-layer.
4e	10YR	6/3	Dark grey vegetation sub-layers.
4f	10YR	6/2	A grey ashy unit.
4g	10YR	7/2	A grey vegetation sub-layer.
4h	10YR	5/4	A brown vegetation unit.

racemosa, *F. opposita* or *F. coronulata*; P. Bostock, pers. comm., 1992) was also retrieved from XU23. The fruit contains the dried, soft tissue, and shows no evidence of fully developed seeds (Fig. 12). All of these items come from SU4h or the SU4-SU4h interface zone, indicating that SU4h may have been a different depositional unit to SU4. Coupled with the fact that all of the pandanus nuts and leaves also come from this unit, SU4h is interpreted as having been laid immediately before SU4 was deposited. This took place sometime around 900 years BP. The most parsimonious explanation for SU4/4h may thus be that the vegetation-rich SU4h was laid together as a single unit. This involved wedging vegetation between boulders devoid of underlying sediments, thereby creating a localised 'false floor'. The digging stick, sheet of cut bark, and the pandanus nuts were then placed on top of this matted vegetation layer, and the whole lot was then covered with more vegetation (containing some hearth remains). The reasons for this are unknown, but ethnographic parallels are known from the Mitchell River delta (pers. obs., 1992). Here, Aboriginal people are known to bury people's 'rubbish' (including cherished material items) after their death. It is possible that the Mordor Cave SU4/4h layer relates to a similar practice, although this is, at this stage, mere speculation.

Discussion of Mordor Cave

An interesting parallel between both Squares E18 and H10 is the large amount of vegetation recovered from the excavations. Especially important is the presence of a bracket fungus from XU2 of Square E18, and a fig from XU23 of Square H10 (dated to approximately 900BP). The very large numbers of Brush Turkey *(Alectura lathami)* eggshell recovered from both squares and from all SUs may also indicate that the site was used on a seasonal basis, and that it was repeatedly re-occupied during the same time of the year (August-December). 2515 fragments of eggshell were excavated from square E18, and 2340 pieces from square H10, distributed throughout the excavated sequences. A single Brush Turkey feather was also recovered from H10 XU3 (Fig. 13).

It is difficult to relate the E18 stratigraphy to that of H10 given the insufficient number of radiocarbon dates obtained. Nevertheless, the peak occurrence of ochre half-way through the deposit in Square E18, whose base was dated to 1500BP, equates well with peak ochre deposition rates around 900BP in Square H10, and may indicate that most of the paintings at the site were undertaken around that time. There is no evidence for any rock art activity at the site having been undertaken before approximately 1500BP. Nevertheless, the presence of a painted pig indicates that cave painting continued into contact times.

Hearth Cave

Hearth Cave is located towards the northern end of the Mitchell-Palmer limestone belt, 9km south of the Palmer River. It was recently rediscovered during speleological explorations by the Chillagoe Caving Club, who report (1988:62):

> Located on 01/04/83 by M. Andersen on north eastern end of tower .... A phreatic slot leading back into tower, 3m wide at entrance. Floor is moss and fern covered. Slot develops to the rear far enough to provide shelter from rainfall. In the small narrow section at the back is a significant ash pile, 2m by 2m and 200mm to 300mm higher than the rest of the floor. Eroded sections of this floor shows evidence of broken bones, a possible kitchen midden.
>
> The walls have a number of Aboriginal paintings, some superimposed on each other on the left hand wall. Observed were a boomerang in white and other paintings vertical scrapings with small numbers at lesser angles. They have been apparently made by someone standing, as they are in easy reach at waist level to hand outstretched in height. Exposure is 2m long by 1m high. Right hand side has scrapings, 12 or so scratches but nothing of real significance. Cave is an archaeological site.

Subsequent recording of the site revealed a greater number of paintings and engravings than initially outlined by the Chillagoe Caving Club,

TABLE 7. List of materials excavated from Mordor Cave, Square H10.

XU	SU	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1	1	279	4.7	5	103.0	148.2	1.7	0.7	0.25	8.6	61.8	16	20.2				0.3	13	1.4	109	1								
2	1	97	1.7	2	36.4	135.3	1.0	0.3	0.25	0.5	17.3	3	0.4				0.1	10	0.4	46	3								
3	3	393	6.3	6	255.0	158.2	5.1	1.9	0.25	1.4	64.5	22	3.5				0.3	28	2.5	185									
4	3	386	5.7	6	106.1	188.6	3.9	1.8	0.25	1.2	27.4	6	7.5				0.4	26	1.5	137									
5	3	339	6.2	7	124.2	255.6	2.8	2.7	0.25	1.7	53.1	7	1.7				0.2	24	2.4	173	4								
6	3	554	7.6	8	234.0	220.0	6.3	2.9	0.25		60.6	9	7.9	1			0.1	20	4.0	238	4								
7	3/4	481	7.0	7	188.6	178.6	4.0	3.2	0.25	1.6	59.8	20	5.4				0.2	17	3.5	216		2.1							
8	4	371	4.6	7	94.2	240.8	3.9	1.8	0.23	2.6	48.6	13	3.6				0.1	9	2.5	146	1			1					
9	4	159	3.2	3	111.7	155.4	3.3	4.0	0.19	1.3	32.7	3	0.3				0.1	13	1.4	99	1								
10a	4	157	2.7	3	52.6	119.4	2.6	4.1	0.09	0.8	25.9	9	2.1				0.1	8	1.4	83									
10b	4	13	0.3	1	16.4	69.6	0.1	2.8	0.01	1.5	3.9	1	0.4						<0.1	1	4								
10c	4/4f	25	0.5	1	16.1	21.3	0.1	2.9	0.03	0.4	5.9	1	0.2				0.1	6	0.2	8	1								
11	4	199	3.6	4	60.9	213.3	3.5	2.5	0.14	0.7	49.0	6	2.4				0.1	10	1.5	93	2								
12	4	209	3.5	4	85.3	390.6	1.2	4.5	0.12	1.0	33.2	3	1.8				0.1	6	1.7	91	3								
13	4	195	3.5	4	153.4	329.7	1.1	5.1	0.11	2.4	56.8	5	2.3				0.1	9	1.1	74									
14	4	159	3.0	4	99.0	258.4	1.3	3.8	0.10	2.4	19.6	7	5.8				0.1	10	0.8	47									
15	4	92	2.2	3	62.5	213.3	0.8	2.7	0.09	0.1	23.0	2	0.1				0.1	5	0.8	26									
16	4	107	2.5	3.5	61.8	189.8	3.4	3.5	0.09	0.5	24.9	6	2.7				0.2	10	0.4	26									
17	4	811	3.5	4.5	55.3	263.5	2.0	4.7	0.09	1.8	19.4	7	4.3				0.1	7	0.1	15									
18	4	162	2.5	4	121.0	249.8	5.9	5.2	0.09	4.5	6.6	2	0.6				<0.1	2	0.1	15									
19	4	88	1.8	3	15.2	318.6	4.9	5.4	0.07	4.5	11.0	3	3.3				<0.1	3	0.1	14									
20	4	146	2.1	5	29.9	277.8	2.8	4.5	0.07	1.3	14.8	4	0.7				0.1	5	0.2	27		36.9							
21	4	221	2.6	5	72.8	224.1	2.6	4.2	0.07	0.2	20.0	1	0.1						0.1	11	1	238.6							
22	4	405	3.3	5	101.8	326.3	3.7	8.2	0.07	2.0	14.1	3	0.1				0:1	7	0.2	29	2		1		1				
23a	4/4h	71	?	?	34.6	242.5	0.4	5.8	0.06	1.3	5.9	1	0.1		<0.1		0.1	2	0.3	17	1		2						
23b	4h	3	0.3	0.1	1.5	3.1	<0.1	1.4	0.01		0.4												1						
24	4h	227	2.8	9	94.9	456.5	0.7	3.9	0.07	0.2	13.4	1	0.1		0.6				0.4	10	2		1						2
25	4h	32	0.1	3	51.6	184.0	4.7	4.2	0.08	0.3	5.9					0.3	<0.1	1	0.3	4		2.9	1			1			
26	4h	185	4.1	9	212.3	455.9	2.9	5.5	0.16	0.7	18.2				0.2		0.1	7	1.3	54	1		5				1	610.4	4
27	4h	771	3.8	5	41.2	282.8	8.3	6.1	0.18	6.6	19.6	8	2.0			1.1	0.1	4	1.2	42	5		1						1
28	4h	280	2.5	3	36.7	210.6	1.5	12.6	0.22	3.8	14.8	2	0.6						1.1	42	2								

1=residue >3mm (g); 2=sediments excavated (kg); 3=sediments excavated (litres); 4=charcoal (g); 5=other organics (g); 6=land snail (g); 7=mean thickness of XU (cm) 8=area excavated (m^2) 9=mussel shell (g); 10=burnt earth (g); 11=flaked stone artefacts (#); 12=flaked stone artefacts (g); 13=feathers (#); 14=crustacean (g); 15=ochre (g) (XU25=2 pieces, XU27=1 piece); 16=burnt egg shell (g); 17=burnt egg shell (#); 18=unburnt egg shell (g); 19=unburnt egg shell (#); 20=seeds (#); 21=burnt stone (g); 22=leaves (#); 23=bone points (#); 24=wooden digging sticks (#); 25=sheets of cut bark (#); 26=grinding stones (#); 27=grinding stones (g); 28=pandanus nuts (#).

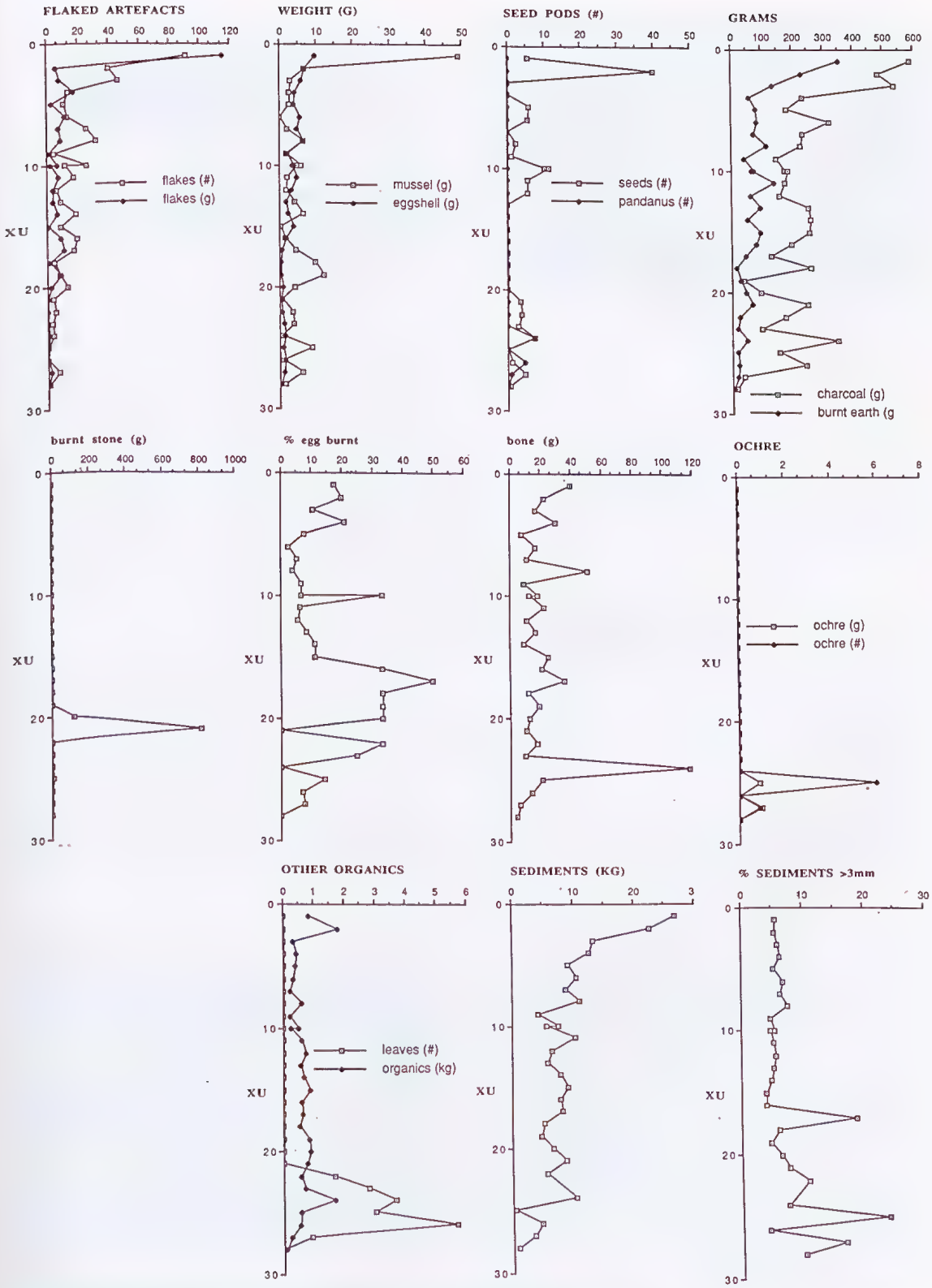

FIG. 10. Mordor Cave, Square H10, deposition rates (per m^2/cm of deposit) and proportions of burnt eggshell.

TABLE 8. Mordor Cave, Square H10: deposition rates (per m^2 per cm of deposit),and proportions of burnt eggshell.

XU	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	26.9	5.6	9.7	588.6	353.1	91.4	115.4					49.1	847	697	9.7	17.6	5.7	40.0						
2	22.7	5.4	13.3	485.3	230.7	40.0	5.3					6.7	1804	747	6.7	20.0	40.0	22.7						
3	13.3	5.9	10.7	536.8	135.8	46.3	7.4					3.0	333	448	5.9	10.7		17.1						
4	12.7	6.3	8.7	235.8	60.9	13.3	16.7					2.7	419	362	4.2	21.1		30.0						
5	9.2	5.2	4.2	184.0	78.7	10.4	2.5					2.5	379	292	3.9	7.7	5.9	7.9						
6	10.5	6.8	8.7	322.8	83.6	12.4	10.9						303	356	5.7	2.4	5.5	16.6	1.4					
7	8.8	6.4	5.0	235.8	74.8	25.0	6.8		2.6			2.0	223	291	4.6	5.4		11.3						
8	11.1	7.5	9.4	227.5	117.4	31.4	8.7					6.3	582	374	6.3	3.8	2.4	51.0						
9	4.2	4.7	4.3	147.0	43.0	3.9	0.4					1.7	205	147	2.0	6.7	1.3	9.3						
10a/b	7.6	5.4	6.8	173.8	75.1	25.2	6.3					5.8	476	232	3.8	6.7	10.1	17.9						
10c	5.7	4.7	1.2	185.1	67.8	11.5	2.3					4.6	245	161	3.5	33.3	11.5	12.6						
11	10.3	5.2	10.0	174.0	140.0	17.1	6.9					2.0	609	294	4.6	6.3	5.7	22.3						
12	6.5	5.6	2.2	158.0	61.5	5.6	3.3					1.9	723	180	3.3	5.6	5.6	11.1						
13	5.8	5.3	1.8	253.6	93.9	8.3	3.8					4.0	545	137	1.8	8.3		16.5						
14	7.9	5.0	3.4	260.5	51.6	18.4	6.1					6.3	680	150	2.4	11.1		9.2						
15	9.1	4.0	3.3	257.2	94.7	8.2	0.4					0.4	878	128	3.7	11.1		25.1						
16	7.9	4.1	10.8	196.2	79.0	19.0	8.6					1.6	603	114	1.9	33.3		21.0						
17	8.3	18.8	4.7	130.7	45.9	16.5	10.2					4.3	623	52	0.5	50.0		35.5						
18	5.3	6.1	12.6	258.5	13.9	4.3	1.3					9.6	534	36	0.3	33.3		11.8						
19	4.8	4.7	13.0	40.2	29.1	7.9	8.7					11.9	843	45	0.4	33.3		18.8						
20	6.7	6.5	8.9	94.9	47.0	12.7	2.2		117.1			4.1	882	102	1.0	33.3		12.4						
21	8.8	7.8	8.8	247.6	68.0	3.4	0.3		811.6			0.7	762	37	0.3	0.0	3.4	10.5						
22	5.7	10.9	6.4	177.4	24.6	5.2	0.2					3.5	569	63	0.5	33.3	3.5	17.2		1.7	1.7			
23	?	?	1.1	99.4	17.0	2.9	0.3					3.7	697	55	1.2	25.0	2.9	9.5		2.8		0.1		
24	10.3	7.5	2.6	347.6	49.1	3.7	0.4					0.7	1672	37	1.5	0.0	7.3	117.6		3.7		2.2	7.3	
25	0.3	24.1	14.0	153.6	17.6				8.6	6.0	0.9	8.9	548	15	1.0	14.3		21.1		3.0				3.0
26	4.7	4.3	3.3	241.3	20.7			1.1				0.8	518	69	1.6	7.1	1.1	14.0		5.7		0.2	4.6	
27	3.5	16.9	7.6	37.5	17.9	7.3	1.8			0.9	1.0	6.0	258	42	1.2	7.7	4.6	6.0		0.9			0.9	
28	0.9	10.1	0.5	13.2	5.3	0.7	0.2					1.4	76	15	0.4	0.0	0.7	4.3						

1=sediments excavated (kg); 2=% sediments 3mm; 3=land snail (g); 4=charcoal (g); 5=burnt earth (g); 6=flaked stone artefacts (#); 7=flaked stone; artefacts (g); 8=grinding stones (#); 9=burnt stone (g); 10=ochre (#); 11=ochre (g); 12=mussel shell (g); 13=other organics (g); 14=egg shell (#); 15= egg shell (g); 16=% egg shell burnt (by weight); 17=seeds (#); 18=bone (g); 19=feathers (#); 20=leaves (#); 21=wooden digging sticks (#); 22=crustacean (g); 23=pandanus nuts (#); 24=sheets of cut bark (#).

with thirteen figurative paintings, one track painting, two non-figurative peckings and 812 abraded grooves (including twelve tridents) being determined (Figs 14,15). In addition, numerous weathered peckings are evident subimposed under a series of paintings, but their quantification and precise identification could not be determined due to their advanced stage of deterioration.

Hearth Cave was chosen for excavation because of the presence of patinated peckings at the site. Non-figurative peckings similar to those found at Hearth Cave are relatively rare in the Mitchell-Palmer region, and were believed to have considerable antiquity at the Early Man site near Laura (Rosenfeld et al., 1981). Consequently, a deep sequence was anticipated from Hearth Cave. Furthermore given that paintings occur in superimposition over the peckings, the recovery of localised in situ ochre should reveal both the antiquity of the paintings and a minimum date for the peckings at the site.

Excavation, Stratigraphy and Dating

Four juxtaposed 50cm × 50cm test pits were excavated, two of which were located against the cave wall in order to determine whether or not rock art continued below the shelter floor (Fig. 16). Only one square (Test Pit 3), however, has been fully sorted and analysed, and consequently this report does not deal with data excavated from the other three squares. It is notable that preliminary analysis of the excavated material from the

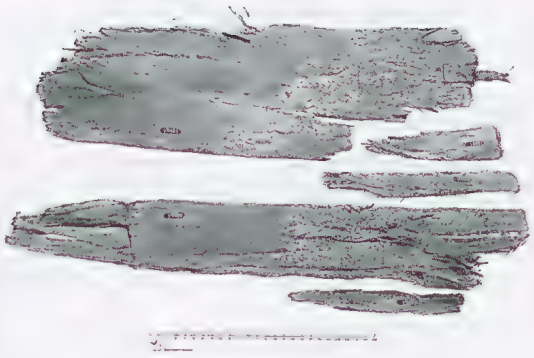

FIG. 11. Mordor Cave, large piece of cut bark excavated from XU25, Square H10.

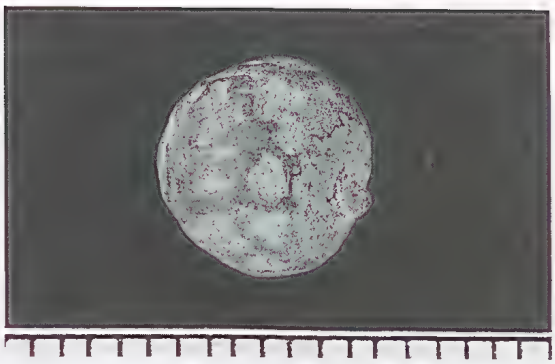

FIG. 12. Mordor Cave, fig excavated from XU23, Square H10 (scale in 2mm units).

other three squares is consistent with temporal trends observed from Test Pit 3.

Test Pit 3 revealed five stratigraphic units, the first four of which were identified during the course of the excavation (Fig. 17). SU5, the basal layer, is indistinct and was only identified whilst section-drawings were being undertaken, after the excavation was completed. The layers are described in Table 10.

Radiocarbon Dates

Four radiocarbon dates were obtained, two of which come from Test Pit 3, the other two from Test Pit 2: 2360±70BP (Wk-1716), on charcoal collected from the sieves from an excavation unit located 18.9 to 22.0cm below the ground surface. $\partial^{13}C$=-26.5‰. This date comes from near the top of SU3 in Test Pit 2; 3494±84BP (R 14023 NZA 1383). This is an AMS date obtained on charcoal from the sieves, located 36.4 to 40.0cm below the ground surface. It was obtained from slightly below the surface of SU4b in Test Pit 2. $\partial^{13}C$=-25.9‰; 4100±120 (Beta-54024), obtained on charcoal collected from the sieves. It dates excavation unit 14a (SU4b), located in Test Pit 3, 40.6 to 45.7cm below the ground surface; 21,500±250 (Wk-1719), a radiocarbon date obtained from land snails (Xanthomelon sp.) located 51.4 to 57.1cm below the ground surface (XU16a). It dates the SU4b-SU5 interface (Test Pit 3). $\partial^{13}C$=-7.2‰.

Cultural Materials

Unfortunately it is not possible to determine deposition rates for the earliest times represented by the Hearth Cave excavations, as radiocarbon dates are not available for the basal units. By assuming a *minimum* of 21,500 years of occupation, however, *maximum* deposition rates can be calculated for the earliest occupational deposits, and temporal patterns can then be explored. It is stressed, however, that the calculation of such rates are for heuristic purposes only. They are employed to determine temporal trends rather than absolute, synchronic values.

Given the uneven nature of the stratigraphic

FIG. 13. Mordor Cave, feather excavated from XU3, Square H10 (scale in 2mm units).

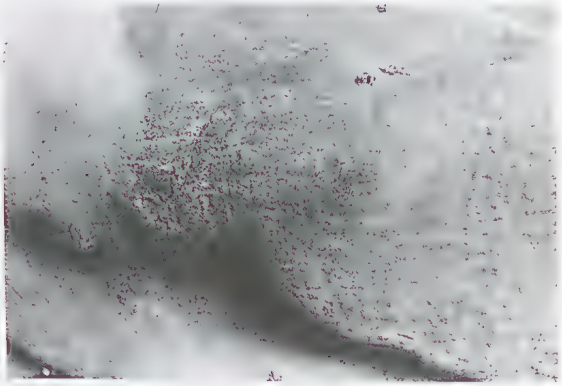

FIG. 14. Hearth Cave, rock wall showing evidence of very weathered peckings and paintings.

TABLE 9. Mordor Cave faunal remains: Minimum Numbers of Individuals (MNI), Square H10 (after Dagg, 1992). Question marks indicate the presence of identified species which are believed to be post-depositional intrusions into that unit (for reasons outlined in Dagg, 1992). P=present.

Species	SU1	SU3	SU3/4	SU4	SU4/4F	SU4/4H	SU4H	Total
Macropus robustus	0	0	0	0	0	0	1	1
Macropus agilis	0	2	0	2	0	0	1	5
Petrogale sp.	0	1	?	3	0	0	3	7
Pseudocheirus peregrinus	1	?	0	0	0	0	0	1
Trichosurus vulpecula	1	0	0	1	0	0	0	2
Peramelidae	0	1	0	2	0	0	0	3
Dasyuridae	0	1	0	0	0	0	0	1
Uramys caudimaculatus	0	0	0	2	0	0	0	2
Other Muridae	1	1	0	6	1	0	2	11
Canis familiaris	0	1	0	0	0	0	0	1
Varanus sp.	0	0	0	1	0	0	0	1
Agamidae	0	1	0	?	0	1	1	3
Scincidae	1	1	0	1	0	0	1	4
Boidae	1	0	0	1	0	0	0	2
Elapidae	0	1	0	0	0	0	0	1
Teleostomi	1	0	0	0	0	0	1	2
Velesunio sp.	P	P	P	P	P	P	P	
Crab	0	0	0	0	0	?	1	1
Xanthomelon sp.	P	P	P	P	P	P	P	
Alectura lathami egg	P	P	P	P	P	P	P	
Alectura lathami	0	1	0	0	0	0	0	1

units near the southern end of the square, especially where SU2 dips down to form a depression, the calculation of deposition rates was only attempted for those parts of the pit where strata are laid approximately horizontally. Table 11 presents the raw data excavated from Test Pit 3, whilst Table 12 transforms this data to deposition rates for each spit (excavation unit). In Table 13, a similar procedure is attempted for each stratigraphic unit.

Although occupation at Hearth Cave began sometime before 21,500±250BP, sedimentation rates peaked between approximately 3500BP and 2500BP, after which they again decreased. Deposition rates of all cultural materials show a similar pattern, being low until approximately 3500BP, and subsequently increasing until 2500-2000BP, after which they decreased slightly and remained relatively stable from then on (Tables 11,12, Fig. 18).

The Hearth Cave bone has not yet been identified to species, but it is notable that very large

TABLE 10. Stratigraphic Units (SUs) from Hearth Cave, Test Pit 3.

SU Description

1 The surface layer, consisting of loose, ashy sediments containing leaves, twigs and cultural materials.

2 Similar to SU1, but sediments are more compact. Charcoal and mussel shell are very abundant, especially immediately above SU3. Sediments are ashy silts. Unlike SU1, there are virtually no leaves or twigs in SU2. The boundary with SU1 above is marked. Towards the southern parts of the excavation, SU2 dips down, forming a depression where charcoal, burnt earth and mussel shell are particularly abundant. It is possible, but not certain, that this depression represents a hearth.

3 Extremely gravelly layer, whose boundary with SU2 above is distinct. Given the coarseness of sediments in SU3, it is thus possible that this layer represents a lag or deflated deposit. This is supported by the considerably larger mean weight of stone artefacts excavated from SU3 than from the other SUs, implying that fine sediments (including very small stone artefacts) have been washed away. Given that deposition rates of cultural materials peak during SU3 times, this may indicate that their original densities should in reality be even greater. Rootlets are common at the interface between SU2 and SU3. Cultural materials were identified in situ throughout SU3.

4a Silty clay containing very large numbers of land snails (especially *Xanthomelon* sp.). Some gravel is present, but in significantly smaller numbers than in SU3 above. SU4a is localised within Test Pit 2 only, and does not appear in Test Pit 3.

4b SU4b consists of silty clays containing cultural materials. Some very fine gravel occurs, but as was the case with SU4a, they are not as numerous as in SU3.

5 Humid clay containing numerous small calcium carbonate concretions. Although SU5 continues beyond the base of the pit, excavation was stopped because no cultural materials were noted in situ within this layer. Subsequent analysis of materials in the laboratory, however, proved that SU5 is not culturally sterile, and investigations will therefore be resumed at a later date to determine the nature of early deposits at Hearth Cave. The fact that basal occupation was not reached does not, however, affect the thrust of this paper, nor the conclusions reached here.

TABLE 11. Hearth Cave: list of materials excavated and information on sediments.

XU	SU	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	1	44	39.6	129.4	161.1	3.3	4.4	26.3		12.5	41	31.0		9.5	9	4	5.9	2750	4.9	0	1.6	1.6	0.84
2	1	106	33.8	179.0	223.1	9.6	10.1	63.1		44.8	53	12.6	1	19.0	8.75	10	11.3	2750	2.8	1.6	4.9	3.3	0.32
3	1	47	34.4	53.1	13.3	3.8	1.2	28.8	40.4	22.3	24	7.0		2.3	9	5	4.7	2750	0.4	4.9	5.8	0.9	0.73
4	2	102	78.5	109.4	32.8	9.1	9.5	42.5		46.6	71	20.7		7.0	9	10	11.6	2700	1.2	5.8	9.2	3.4	0.77
5	2	119	55.6	131.7	19.4	13.1	2.6	9.4	68.4	47.0	80	92.9	1	27.4	8.5	12	12.4	2700	0.7	9.2	12.4	3.3	0.47
6	2	90	25.9	105.1	36.1	12.7	5.5	22.7		49.7	71	31.6		19.0	8.5	11	11.6	2700	1.0	12.4	15.1	2.7	0.29
7	2	104	30.0	69.0	15.0	10.3	1.3	5.2		45.6	39	8.7	3	21.8	8.5	10	11.0	2650	0.8	15.1	17.7	2.5	0.29
8b	2	13	0.8	3.6	2.5	3.0	0.4	0.5		7.8	7	0.4		2.0	8.5	5	5.3	1100	0.2	17.7	22.3	4.1	0.06
10b	2	56	10.4	35.3	67.2	7.1	1.3	7.0		16.3	22	4.4		5.4	8.5	10	10.2	1900	1.3	22.3	25.9	3.6	0.19
11b	2	30	4.4	5.6	14.4	4.4	0.4	0.2		8.1	3	0.1		1.5	8.5	6	6.0	1350	0.2	25.9	29.7	3.8	0.15
12b	2	24	4.6	8.8	43.7	6.3	0.5	0.1		8.5	16	1.3		12.2	8.5	10	11.0	1300	0.3	29.7	36.1	6.4	0.19
13b	2	21	3.0	8.9	30.7	2.3	0.1	0.1		1.6	2	0.4		3.1	8.5	6	6.6	820	0.2	36.1	40.4	4.3	0.14
14b	2	12	1.9	9.9	62.3	1.5	0.1	0.1		1.2	3	0.7		1.0	8.5	4	6.8	750	0.2	40.4	44.5	4.1	0.16
15b	2	14	2.0	5.1	33.4	1.0	0.1			0.5				5.6	8.5	5	4.5	470	0.1	44.5	50.3	5.8	0.14
16b	2	6	0.2	1.2	51.6	0.8	0.1			0.4	2	0.1		0.2	8	5	5.7	330	0.1	50.3	57.4	6.9	0.03
8a	2/3	78	25.8	37.5	52.4	4.6	0.9	4.9		26.4	26	6.1		1.4	8.5	5	4.7	1550	0.6	17.7	18.5	1.3	0.33
9	3	72	44.4	137.1	283.9	3.3	0.6	4.7		10.9	31	24.9		1.9	9	6	6.4	810	2.6	18.5	21.6	3.2	0.62
10a	3	17	47.9	102.6	377.0	1.2	0.7	1.1		3.3	16	8.6		1.2	8.5	4	5.8	850	1.8	21.6	25.3	3.7	2.82
11a	3	49	90.3	189.5	647.1	2.2	1.3	16.1		8.8	60	80.2		1.3	8.5	8	10.9	1500	1.9	25.3	29.8	4.5	1.84
12a	3	30	80.1	143.9	631.6	2.9	1.9	2.9		4.9	28	25.0		1.5	8.5	8	9.9	950	2.6	29.8	36.5	8.1	2.67
12c	3/4b	19	6.8	65.4	294.4	2.8	1.3	0.8		4.6	17	9.6		3.3	8.5	5	5.8	450	1.0	29.8	36.9	7.1	0.36
13a	3/4b	25	18.7	65.2	63.1	1.9	2.1	0.5		4.1	24	8.0		2.4	8.75	?	9.8	1800	1.5	37.3	40.6	3.3	0.75
14a	4b	3	0.1	17.9	414.4	1.3	0.1	0.4		1.1	2	0.2		0.6	9	8	9.7	1950	1.0	40.6	45.7	5.1	0.03
15a	4b/5	5	0.2	15.9	213.9	1.2	0.2	0.1		1.1	3	0.1		1.7	8.25	11	13.5	2200	1.2	45.7	51.4	5.7	0.04
16a	4b/5	38	3.5	16.3	151.2	0.7	0.1	2.2		0.2	2	1.1		0.4	8.5	12	15.4	2350	1.1	51.4	57.1	5.7	0.09
17	4b/5	2	0.1	1.7	78.7	0.2	0.1			0.1	4	0.1		0.7	8.25	12	14.0	2750	1.2	56.7	61.5	4.7	0.05
18	5	12	0.5	4.2	41.9	0.6	0.2			0.1	3	1.7		4.1	8.5	14	16.9	2750	2.1	61.5	66.6	5.1	0.04
19	5	6	0.2	0.8	36.6	0.1				0.1	8	2.4		2.4	8.25	10	11.7	1250	1.3	66.6	72.9	7.9	0.03
20	5	5	0.2	1.8	2.4	0.1	0.1				7	0.5		0.1	8.25	7	8.2	1250	0.8	72.9	78.2	5.4	0.04
21	5			0.2	0.1						1	0.1		0.1	8.25	?	3.7	625	0.6	78.2	83.4	5.2	

1=stone artefacts (#); 2=stone artefacts (g); 3=bone (g); 4=land snail (g); 5=egg shell (g); 6=mussel shell (g); 7=burnt earth (g); 8=burnt stone (g); 9=charcoal (g); 10=ochre (#); 11=ochre (g); 12=bone points (g); 13=other organics (g); 14=pH; 15=volume (litres) dug; 16=weight (kg) dug; 17=area (cm^2dug; 18=residue >3mm (kg); 19=mean start depth below surface (cm); 20=mean end depth below surface (cm); 21=mean thickness of XU (cm); 22=mean weight of stone artefacts (g).

numbers of Brush Turkey egg shell occur in all cultural layers. Brush Turkeys lay their eggs from the end of the dry to the beginnings of the wet season (August-December), offering a reliable seasonal marker for when the site was used (W. Longmore, pers. comm., 1992). Although this question needs further attention, it is possible that the repeated high numbers of egg shell at Hearth Cave implies great continuity of a seasonal settlement system whereby rockshelters from the region were repeatedly occupied during the wet season. This does not deny the possibility, however, that the site was also used during other times of the year. Further research into this issue will have to await systematic investigation of the faunal material from Hearth Cave and elsewhere, as well as investigations in other sites from the region (including both rockshelter and open sites).

The stone artefacts are largely 'amorphous', although technologically they may possess highly diagnostic characteristics (this remains to be investigated). Only two formal stone tool 'types' were identified from the excavation: a fragment of 'edge-ground axe' from XU5 (1100-1450BP), and a 'burren adze slug' from XU4 (700-1100BP). Given their low numbers, however, it is difficult to make any generalisation about typological change in the stone tool assemblage from the site. It may nevertheless be significant to note that the 'burren adze' found at Hearth Cave was dated to around the same time as their appearance in other sites excavated from south-east Cape York Peninsula (David, in prep.).

The temporal distribution of in situ ochre is similar to the distribution of other types of cultural items. Numbers of ochre fragments peak during the last 3500 years, and high levels are maintained until ethnohistoric times. The very low ochre deposition rates before approximately 3500BP are likely to signify that the cave paintings currently visible at the site post-date this time, although the excavations have furnished no

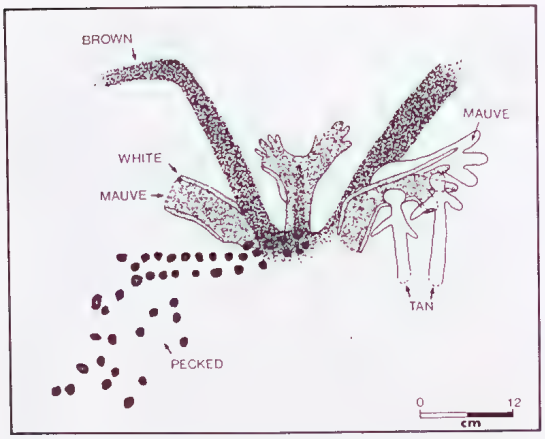

FIG. 15. Hearth Cave, freehand recording of part of the main painted and pecked panel. Not to scale.

direct indication of the age(s) of the underlying – and therefore older – peckings.

The increases in deposition rates documented from Hearth Cave after 3500BP include the following: 1, Increased sedimentation rates, which Hughes (1977) and Hughes & Lampert (1982) have argued may be related to increases in occupational intensities; 2, Increases in the deposition rates of bone, charcoal and burnt earth, which together may imply increased rates of hearth establishment and firing activity, and increases in the amounts of food consumed and discarded at the site; and 3, Increases in ochre, which implies an increase in painting activity.

It is, nevertheless, difficult to determine further the exact characteristics of the temporal frameworks involved. This is due to an absence of fine stratigraphy at the site, making it difficult to obtain discrete temporal units which can then be used to construct a chronological framework.

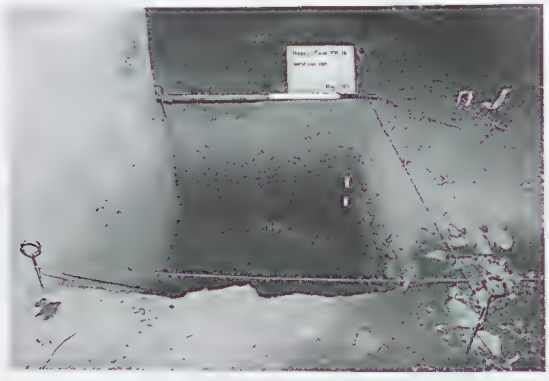

FIG. 16. Hearth Cave, the excavation pit, showing the west section (scale in 5cm units).

Consequently, we have resorted to the use of a depth-age curve to calculate temporal trends. Furthermore, the availability of three dates from 2360±70 to 4100±120BP has enabled a fairly good assessment of changes around this time.

DISCUSSION

The distribution of in situ ochres at Mordor Cave and Hearth Cave is comparable to their distributions in other excavated sites from southeast Cape York Peninsula. In all sites, peak ochre deposition rates occur late in the sequence and continue to increase until very recent times. This is the case for the following:

1, the Early Man rockshelter, where in situ ochres increase significantly after either 5000BP or during the last two millennia or so (the precise dating is debatable because of chrono-stratigraphic uncertainties) (Rosenfeld et al., 1981; David, 1991b);

2, Green Ant Rockshelter (Koolburra Plateau), where they increase dramatically after 2500BP (Flood & Horsfall, 1986; Flood pers. comm., 1991);

3, Mitchell River Cave (Mitchell River), where the only fragment of ochre was obtained from deposits dating to the last 1000 years (David, 1991a);

4, Echidna's Rest (Chillagoe), where ochre deposition rates double after 3000 years ago, and continue to increase during the last 700 years (David, 1990).

The implications of this are that cave paintings in southeast Cape York Peninsula pertain particularly to the mid to late Holocene. Painting conventions vary greatly across space throughout southeast Cape York Peninsula, indicating a highly regionalised social landscape during this

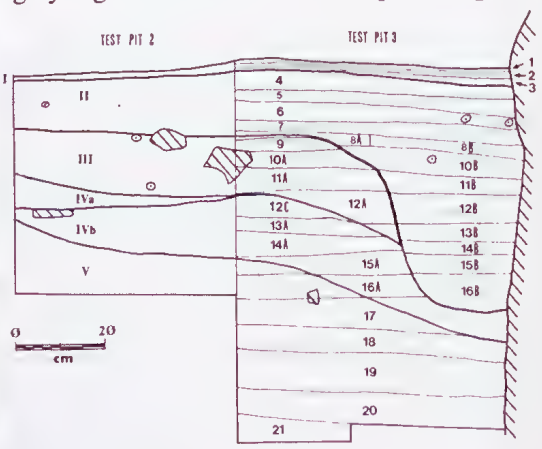

FIG. 17. Hearth Cave, stratigraphy, east section.

TABLE 12. Hearth Cave: deposition rates by XU (per m^2 per 100 years). Note that rates could not be calculated for XUs below XU15a, as no radiocarbon determinations were obtained from the lower XUs.

XU	SU	1	2	3	4	5	6	7	8	9	10	11	12
1	1	200	80.0	67.1	74.5	56.4	235.3	8.0	6.0	22.7	47.8		0.9
2	1	600	96.4	30.7	48.2	11.5	162.7	9.2	8.7	40.7	57.4		0.9
3	1	700	170.9	125.1	87.3	25.5	193.1	4.4	13.8	81.1	104.7	146.9	0.9
4	2	1100	94.4	72.7	65.7	19.2	101.3	8.8	8.4	43.0	39.4		0.9
5	2	1450	125.9	58.8	84.7	98.3	139.4	2.8	13.9	49.7	9.9	72.4	0.9
6	2	1800	95.2	27.4	75.1	33.4	111.2	5.8	13.4	52.6	24.0		0.9
7	2	2100	130.8	37.7	49.1	10.9	86.8	1.6	13.0	57.4	6.5		0.9
8a	2/3	2150	1006.5	332.9	335.5	78.7	483.9	11.6	59.4	340.6	63 2		0.9
9	3	2500	254.0	156.6	109.3	87.8	483.2	2.1	11.6	38.4	16.6		0.9
10a	3	2700	100.0	281.8	94.1	50.6	603.5	4.1	7.1	19.4	6.5		1.9
11a	3	3000	108.9	200.7	133.3	178.2	421.1	2.9	4.9	19.6	35.8		1.5
12a+c	3/4b	3500	70.0	124.1	64.3	49.4	299.0	4 6	8.1	13.6	5.3		1.5
13a	3/4b	3850	38.0	28.4	36.5	12.2	99.1	3.2	2.9	6 2	0.8		0.9
14a	4b	8250	0.3	<0.1	0.2	<0.1	2.1	<0.1	0.2	0.1	<0.1		0.1
15a	4b/5	17450	0.2	<0.1	0.1	<0.1	0.8	<0.1	0.1	0.1	<0.1		0.1

1=end years BP for spit 2=stone artefacts (#); 3=stone artefacts (g); 4=ochre (#); 5=ochre (g); 6=bone (g); 7=mussel shell (g); 8=egg shell (g); 9=charcoal (g); 10=burnt earth (g); 11=burnt stone (g); 12=sedimentation (cm).

time (e.g. Rosenfeld, 1982, 1984; David & David, 1988). Considerable support for these findings have been obtained for very recent times from the ethnographic record. More problematic is an apparent, more homogeneous engraving tradition characterised by non-figurative and animal track peckings throughout the region (see Maynard, 1977, 1979). Their probable greater antiquity and relative homogeneity may imply that inter-regional networks were structured differently during earlier times (before the mid Holocene?), although this issue needs to be further investigated by obtaining more secure dates on the engravings themselves. Nevertheless, the repeated occurrence of engravings *underneath* paintings at Laura, the Koolburra Plateau, Chillagoe and elsewhere, indicates that this temporal pattern has so far withstood the test of time (cf. Flood, 1987; Rosenfeld et al., 1981; Woolston & Trezise, 1969). The conclusion that the last few thousand years of prehistory in southeast Cape York Peninsula witnessed a fundamental restructuring of artistic, and therefore probably also socio-cultural, networks appears to be strengthened with every excavation adding further support for a largely late Holocene antiquity of cave paintings. The highly regionalised nature of these paintings contrasts markedly with the relatively homogeneous nature of the preceding engravings.

Related to this question, it is noted that a significant proportion of the excavated faunal remains from Mordor Cave consist of food debris dominated by macropods — *Petrogale* sp., *Macropus agilis* and *Macropus robustus* — and other marsupials (e.g. *Trichosurus vulpecula*). The total absence of macropods from the paintings, and the general non-conformity between the range and relative representation of fauna recovered from the excavations and those represented in the paintings may be of great interest. The implications are that the animals painted on cave walls during the mid to late Holocene are not simply a reflection of dietary breadth, nor simply an indication of the symbolic importance of the hunted and foraged fauna. On the contrary, the two sources of faunal representation — the painted animals and the animals represented in the food debris — represent two distinct information domains, each of which relates to a different set of socio-cultural principals (set within a socio-cultural system or systems). In other words, data obtained from the excavated food remains relates specifically to subsistence behaviour, whereas the painted forms are an archaeological window into a totally different aspect of prehistoric life within a site and region. By investigating the latter we are investigating a system of visual forms structured by socio-cultural convention, a system of symbols whose investigation can reveal something about the nature of symbolic vocabularies but not about their related original meaning contents (cf. Frost et al., 1992). Although rock art has largely been ignored in Australian archaeology until recent times, it is important to note that once different bodies of rock art from a single region (and across space) are dated, continuities and discontinuities in visual conventions can be investigated. This does not require the art having had 'meaning' to its creator in the sense that it was created for a particular reason beyond 'art for art's

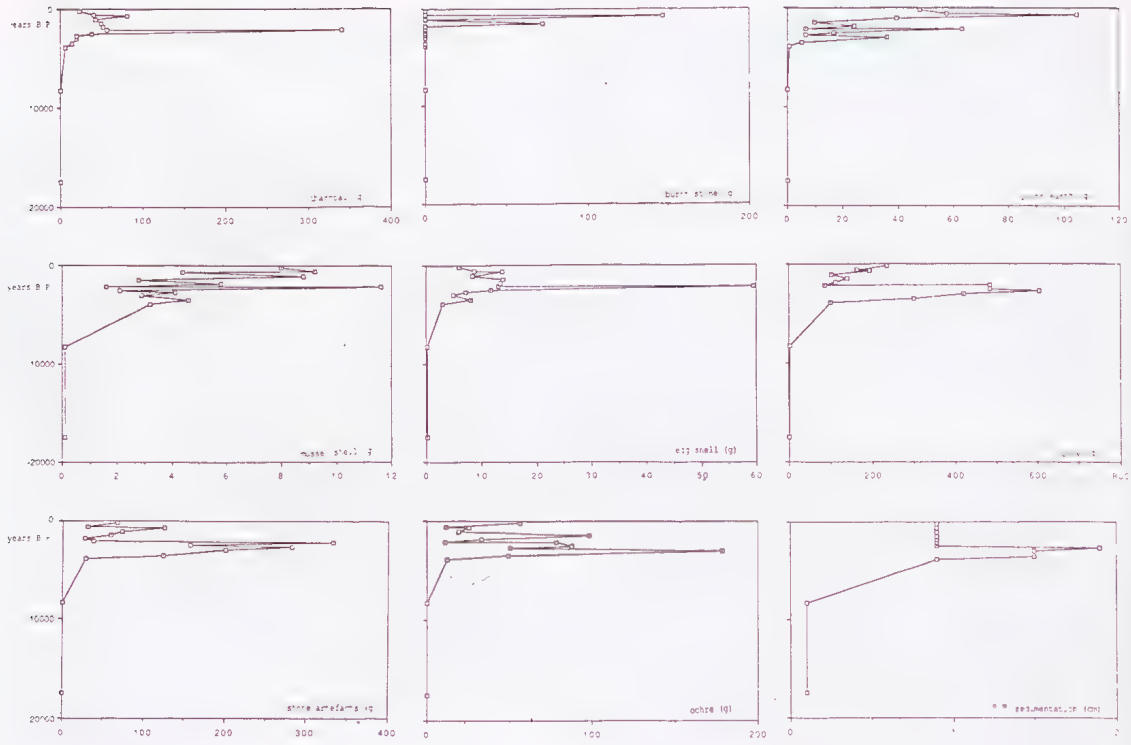

FIG. 18. Hearth Cave, deposition rates by XU (per m²/100 years). Rates for SU5 are maximum rates only, based on the assumption that cultural deposits began 21,500BP. In reality, this is only a minimum date for occupation. Therefore, the temporal trends evident in the curves would be accentuated with longer occupation at the site.

sake', for what is at stake concerns the structuring of socio-cultural imagery, of the ordering of symbols as formal representations and of the portrayal of rock art forms in specific proportions. For example, why are there no recorded macropods in the Mitchell-Palmer rock paintings, especially given their importance in the rock art of Laura to the immediate north? Why does the nature of painted representations change less than 50km to the south of the Mitchell-Palmer region, from a predominantly figurative painting region to a non-figurative one? The implications are that during relatively recent times at least, spatial discontinuities existed in the distribution of socio-cultural conventions relating to rock art through space (David, in prep.). Given that rock art does not necessarily relate to any specific aspect of social life such as subsistence, however, it does not necessarily follow that the documented discontinuities in rock art also represent differences in other social practices. But the regionalised nature of rock art traditions during the late

TABLE 13. Hearth Cave: deposition rates by SU (per m² per 100 years). Note that some XUs are interface spits, and therefore their relative contributions to the various SUs to which they belong have been taken into account in the calculations presented.

SU	XUs	1	2	3	4	5	6	7	8	9	10	11	12
1	1-3	700	102.3	54 6	61.3	26 2	187.7	8.2	8.7	41.4	61.3	21.0	206.5
2	4-8a	2150	242.2	61.4	104.7	42.0	146.5	6.4	26.8	66.0	22.9	17.5	237.5
3	8a-13a	3450	195.2	210.7	128.2	103.9	516.0	5.1	12.0	33.2	17.6		1731.6
4b	12c-17	?9000	12.0	2.4	6.2	2.4	19.2	0.4	0.9	1.3	0.3		117.4
5	15a-21	>21,500	<1.8	<0.1	<1.3	<0.3	<0.9	<0.1	<0.1	<0.1	<0.1		<11.3

1=end years BP 2=stone artefacts (#); 3=stone artefacts (g); 4=ochre (#); 5=ochre (g); 6=bone (g); 7=mussel shell (g); 8=egg shell (g); 9=charcoal (g); 10=burnt earth (g); 11=burnt stone (g); 12= land snail (g).

Holocene implies regionalised symbolic behaviour throughout southeast Cape York Peninsula during that time. The precise nature of this regionalisation — whether it involved broader discontinuities or not — remains unknown. It is therefore to explore such issues that we present this paper, for it is by generating systematic research on past socio-cultural systems in southeast Cape York Peninsula — that is, on the relationship between resource structures, symbolic representations, technological conventions etc., and their continuities and discontinuities across space and through time — that significant new inroads will be made in Aboriginal prehistory.

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A NEW SPECIES OF *LYGISAURUS* DE VIS (REPTILIA: SCINCIDAE) FROM MIDEASTERN QUEENSLAND

PATRICK J. COUPER

Couper, P.J. 1993 06 30: A new species of *Lygisaurus* de Vis (Reptilia: Scincidae) from mideastern Queensland. *Memoirs of the Queensland Museum* 33(1): 163-166. Brisbane. ISSN 0079-8835.

Lygisaurus zuma sp.nov. is from open forests and riparian habitats of the Mackay district, mideastern Queensland. It is distinguished from its congeners by the following combination of characters: midbody scale count 23-24, supraciliaries usually 6, ear lobules flat and low, and palpebral disc large. Faecal analysis shows that this species feeds on small arthropods. In captivity, male *L. zuma* display territorial behaviour and both sexes give a brief, head-bobbing display when establishing themselves in a sunning position. Male *L. zuma* develop a red breeding flush on their throats and tails, which reaches full intensity by late October. A captive female produced two soft-shelled, oval shaped eggs, in mid-November.
☐ *Lygisaurus zuma, Scincidae, new species, open forest, Queensland.*

Patrick J. Couper, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 5 January, 1993.

Ingram and Covacevich (1988) resurrected the genus *Lygisaurus* from the synonymy of *Carlia* to accommodate the small, brown litter-dwelling skinks, which had formed a discrete unit within *Carlia*. They transferred four species (*L. foliorum*, *L. aeratus*, *L. laevis* and *L. macfarlani*) to *Lygisaurus* and described three new species (*L. rococo*, *L. sesbrauna* and *L.tanneri*) from northeastern Queensland. In addition, *Menetia timlowi* (Ingram, 1977) was reallocated to the genus *Lygisaurus*. Subsequently, Greer (1991) changed the generic diagnoses of *Lygisaurus* and *Menetia* and concluded that *L. timlowi* was more closely related to *Menetia* than to *Lygisaurus*. He reassigned it accordingly.

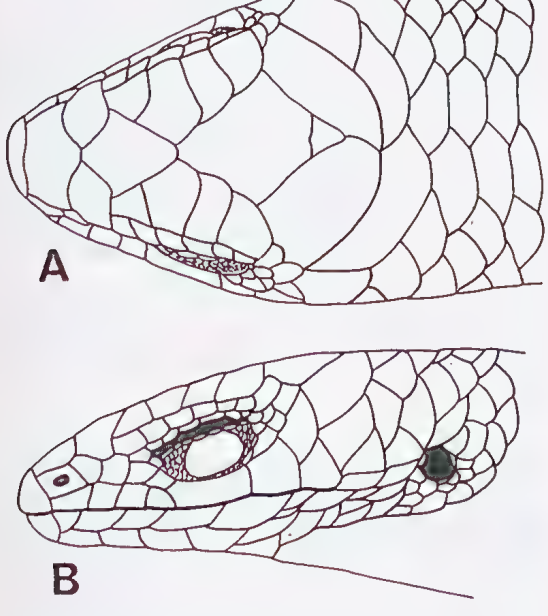

FIG. 1. *Lygisaurus zuma* (J55760). A. Dorsal view of head. B. Lateral view of head.

During recent field surveys north of Mackay, mideastern Queensland, a new *Lygisaurus* closely resembling *L. tanneri* was collected. The new species conforms to the generic diagnoses of Ingram and Covacevich (1988) and Greer (1991). On external features alone, it is readily referable to the genus *Lygisaurus* by the presence of ear lobules, which *Menetia* lacks (Greer, 1991). Further, the number of paravertebral scales in the new species (44-48) is within the range of *Lygisaurus* (39-50), whereas *Menetia* has 52-66 (Greer, 1991). The discovery of a new species of *Lygisaurus*, following a recent revision of this genus, emphasises the importance of field surveys in areas that have been previously overlooked. With the exception of the Eungella rainforest block, the forests of the Mackay area have been largely ignored because researchers have focused their attention on forests further north.

Body measurements and morphological characters follow Ingram and Covacevich (1988). SV = snout-vent length; HW = head width; TL = tail length; HL = hindlimb length. The number of supraciliaries, supraoculars, ear lobules, supralabials and subdigital lamellae have been recorded from both sides of the body. The subdigital lamellae count includes the most distal scale. In addition, the numbers of enlarged nuchal scales and paravertebals have also been counted

FIG. 2. *Lygisaurus zuma* (J56874) Boulder Ck, MEQ (S. Wilson).

(sensu Greer, 1991). All specimens examined are in the Queensland Museum.

Lygisaurus zuma sp.nov.
(Figs 1-4)

MATERIAL EXAMINED

HOLOTYPE: J55760 female, Boulder Ck, via Mt Charlton, MEQ (21°01'S, 148°43'E), collected by P.J. & K.L.D. Couper on 21-23 July 1992.

PARATYPES: J53397, J55761-7, J56874-6, J56883 Boulder Ck, via Mt Charlton, MEQ; J56278, J56280 small knoll immediately WNW of Mt Ossa township, E of where Carey Ck crosses Bruce Highway, MEQ (20°55'S, 148°48'E); J56279 small knoll just east of the Geeberga-Buthurra Rd, 6.7km from where the road meets the Bruce Highway opposite Buthurra, MEQ (21°01'S, 148°48'E); J56765 Neilson Ck, at the base of Mt Blackwood, MEQ (21°01'S, 148°58'E); J56786 proposed Teemburra Ck Dam, near Pinnacle, N of Mackay, MEQ (21°13'S, 148°39'E).

DIAGNOSIS

A medium sized (maximum SV 34mm) *Lygisaurus* (Fig. 2). *L. zuma* sp. nov. has a movable lower eyelid, a character it shares with *L. aeratus*, *L. laevis*, *L. macfarlani*, *L. rococo*, *L. sesbrauna* and *L. tanneri*. *L. zuma* sp. nov. is distinguished from *L. rococo* by midbody scale count (23-24 vs 27-30); from *L. tanneri* by the number of supraciliaries (usually 6 vs usually 7); from *L. aeratus*, *L. laevis* and *L. sesbrauna* by the nature of the ear lobules (flat and low vs sharp); from *L. macfarlani* by the size of the palpebral disc (large, occupying more than half of the lower eyelid vs small, occupying less than half of the lower eyelid), a character which further distinguishes it from *L. laevis*, *L.sesbrauna* and *L. tanneri*.

DISTRIBUTION

The Mackay district, mideastern Queensland (Fig. 3).

DESCRIPTION

SV: 23-34 (N = 18, mean 30.0). Proportions, (% SV): HW, 12-16 (N = 18, mean 14.3); TL, 130-178 (N = 6, mean 151.4); HL, 28-40 (N = 18, mean 35.7). Supraciliaries 6, rarely 5 or 7 (N = 36, mean 6.0). Palpebral disc large, occupying more than half of the lower eyelid. Lower eyelid movable. Ear aperture much smaller than palpebral disc; varying in shape from round to almost

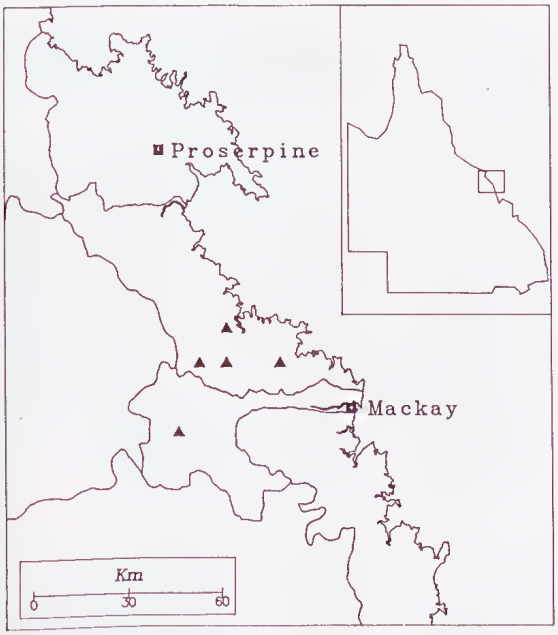

FIG. 3. Distribution of *Lygisaurus zuma*.

horizontal, with low flat lobules around the margin. Supraoculars 4, rarely 3 (N = 36, mean 3.9). Supralabials 7 (N = 36), with the fifth under the eye. Three scales between the second presubocular and the nasal scale. Enlarged nuchal scales 2-3 (N = 18, mean 2.1), with two contacting the parietal shields. Midbody scale rows 23-24 (N = 17, mean 23.7). Number of scales from chin to vent 50-58 (N = 17, mean 53.5). Number of paravertebral scales 44-48 (N = 17, mean 46.6). Number of lamellae under fourth toe 19-23 (N = 34, mean 21.3).

Dorsal colour pattern iridescent grey-brown with longitudinal rows of small black flecks that become more concentrated on the flanks, forming a darker lateral zone. Ventral surface silvery white with a dark edging to the belly scales; chin immaculate. Head coppery with scattered dark blotches. In life, eye pale green with a black pupil. Breeding males have red tails and throats.

Etymology

The name is derived from Montezuma II, the last Aztec emperor, who was a sun-worshipper. The name alludes to the lizard's basking habits. The epithet is to be treated as a noun in apposition.

Habitat

L. zuma lives in the leaf-litter of open forests and associated riparian habitats. J53397, 55760-55767, 56874-56876, 56883 were collected from a mixed, eucalypt-dominated woodland, predominantly comprised of the following species; *Eucalyptus dolichocarpa*, *E. intermedia*, *Pandanus tectorius*, *Ervatamia orientalis*, *Flindersia schottiana*, *Planchonia careya*, *Acacia flavescens*, *Randia fitzalanii*, *Mallotus philippensis*, *Glochidion sumatranum* and *Lophostemon suaveolens* (Fig. 4). J56279 was collected from a stand of *L. suaveolens* with scattered *Eucalyptus platyphylla* and young *M. philippensis*. J56280 is from an *E. intermedia* dominated forest with an understorey of *Lophostemon confertus*. J56765 was collected from a creek-bed containing riverine vegetation, immediately adjacent to a eucalypt dominated woodland. J56786 was taken from an open riparian forest dominated by *Casuarina* sp. J56278 was found in dense leaf litter in a dry gully in a patch of rainforest.

The penetration of open forest species into rainforest is discussed by Covacevich and McDonald (1991). The occurrence of *L. zuma* in rainforest may be an example of this, probably the result of severe drought. Specimen J56278 was collected during September 1992, one of the driest periods on record for the Mackay area. Field surveys conducted in October 1991 failed to find this species in rainforest, despite a total 18 man-days spent in rainforests around Mt Ossa and Mt Charlton.

Habits

Like all *Lygisaurus*, *L. zuma* is a small, ground-dwelling diurnal skink. Individuals seen at Boulder Ck during July 1992 were actively foraging through the litter layer from mid-morning to early afternoon. All observed activity was confined to patches of sunlight. Ground temperature in these sun patches ranged from 24- 28°C.

An examination of four faecal samples showed that *L. zuma* feeds on small arthropods. One of the samples contained two ground spiders of the families Lycosidae and Pisauridae and another two of the samples each contained a single planthopper (Hemiptera: Fulgoroidea). The fourth sample, while containing no prey items, consisted of numerous scales presumably ingested by the skink while sloughing. Specimens kept in captivity readily eat termites, actively avoiding the soldiers and preferring the larger, more succulent workers.

Male *L. zuma* observed at Boulder Ck during July 1992 had not yet developed their full breeding colours. While the lower labials displayed a well developed, red flush, the scales of the throat

FIG. 4. Open forest habitat of *Lygisaurus zuma*,

remained white with only a hint of orange appearing around the margins. Breeding colours develop to full intensity by late October, as was the case with J53397 and J56765, and begin to fade by early December (captive males J56874 and J56876). In captivity, territorial behaviour was evident in males well before breeding colours had fully developed. The larger of two males sharing an enclosure with two females would actively chase the other male whenever contact occurred. Both males and females gave a brief display of head-bobbing as they first established themselves in a sunning position.

Captive female J56883 (SV: 33.9mm) laid two soft-shelled, oval-shaped eggs on 18 November 1992 (± 2 days). The eggs became desiccated and required rehydrating before any measurements could be taken. Egg length ranged from 7.52-7.54mm egg width from 3.85-3.95mm.

ACKNOWLEDGEMENTS

This work was funded by a grant from the National Rainforest Conservation Programme, administered by the Department of Environment and Heritage. I am especially grateful to Duncan Limpus for his efforts in obtaining the first specimen of *L. zuma* from our Boulder Ck campsite. I also wish to thank Peta Woodgate and Lynette Dickfos for typing; Glen Ingram, Jeanette Covacevich and Steve Wilson for critically reading the manuscript; Steve Wilson for his excellent photograph; Gray Cranitch for preparing the photographic figures; David Nebauer for preparation of the map; Peter Thompson for identifying botanical specimens; Geoff Monteith and Kevin Lambkin for identifying insect fragments contained in faecal samples; Michael Cunningham, Kate Couper and Alan Beckman for their assistance in the field; Tim Low and Morgan Thomas for collecting additional material; and Lauren Keim for her assistance in the laboratory.

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A NEW SPECIES OF *UPEROLEIA* (ANURA: LEPTODACTYLIDAE: MYOBATRACHINAE) FROM NORTHEASTERN AUSTRALIA

MARGARET DAVIES, GRAEME F. WATSON, KEITH R. MCDONALD, MICHAEL P. TRENERRY AND GARRY WERREN

Davies, M., Watson, G.F., McDonald, K.R., Trenerry, M.P. & Werren, G. 1993 06 30: A new species of *Uperoleia* (Anura: Leptodactylidae: Myobatrachinae) from northeastern Australia. *Memoirs of the Queensland Museum* **33**(1): 167-174. Brisbane. ISSN 0079-8835.

Uperoleia altissima sp.nov. is from elevated sites on the Atherton and Windsor Tablelands in northeastern Queensland. The species is dentate and the call is short and pulsatile, features that distinguish it from all congeners. □ *Anura, Myobatrachinae, Leptodactylidae, Uperoleia altissima, new species, advertisement call, external morphology, osteology.*

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Uperoleia is a genus of small, fossorial frogs with highly glandular skin and a conservative morphotype. The nominate species, *U. marmorata,* was described by Gray (1841) and prior to 1981 was thought to have a wide ranging distribution throughout northern and eastern Australia. Tyler et al. (1981a,b) revised the genus and raised the number of recognised species from three to 18. They restricted the known distribution of *U. marmorata* to the type locality in northern Western Australia.

Davies et al. (1985) described a further species from the Pilbara whilst Tyler et al. (1986) suppressed *U. variegata* leaving 18 recognised species. These studies were confined to the Northern Territory and northwestern Western Australia and, thus, did not deal in any detail with eastern species (*U. rugosa, U. fimbrianus* and *U. laevigata*). These they restricted to their type specimens and localities, pending revision of the *Uperoleia* in eastern Australia. When this was completed (Davies & Littlejohn, 1986; Davies et al., 1986), *U. fimbrianus* was synonymised with *U. rugosa* and an additional six species were described. Presently, 23 species are recognised within *Uperoleia.*

During the study of eastern Australian *Uperoleia* a number of specimens were located in museum collections that could not be positively identified. Amongst these were five specimens in the Queensland Museum collection taken near Atherton, NE Queensland. These frogs appeared to be dentate, so resembling *U. fusca* in Eungella National Park near Mackay, mideastern Queensland. However, they were too poorly preserved to permit positive identification.

In late January 1991, M.D., G.F.W. and K.R.McD. visited the Atherton Tableland and located a species of *Uperoleia* in the Millstream National Park. The species was dentate and conspecific with the indeterminate specimens encountered previously and with others collected at later dates from this site and the Windsor Tableland. Here we describe it as a new species.

MATERIALS AND METHODS

Material cited here is deposited in the collections of the Queensland Museum, Brisbane (QM), South Australian Museum, Adelaide (SAM), Museum of Natural History, University of Kansas (KU), and American Museum of Natural History, New York (AMNH). Measurements of specimens follow Tyler et al. (1981a). Measurements taken (in mm) were: eye diameter (E); eye to naris distance (E-N); internarial span (IN); snout to vent length (S-V); tibia length (TL).

Osteological data were obtained from cleared and stained material after the methods of Davis & Gore (1947) and Dingerkus & Uhler (1977).

The tape recording was made using a Sony TC-D5PRO cassette recorder (tape speed 4.76 cm/s) and Beyer M-88 cardioid dynamic microphone. Air wet bulb temperature (the effective temperature of a frog calling on land) was measured at the calling site using an electronic thermistor thermometer (Takara Digimulti Model

D611). The recording was analysed on a DSP 5500 digital Sona-Graph (Kay Elemetrics Corp.) using the in-built setup #10, with playback on a Nakamichi Dragon cassette recorder. Overall variations in tape speed (i.e. from recording to playback) are estimated at less than 0.5%; and the frequency responses of all audio-electronic components are close to linear within the relevant frequency range determined (based on the manufacturer's specifications). For each call, three primary attributes were determined: (i) duration as the interval from the beginning of the first pulse to the end of the last pulse (ms); (ii) number of pulses per note (direct count); and (iii) dominant frequency (Hz) as the maximum value of the spectrum of power between the cursors for the whole note. One derived attribute was determined — pulse rate [pulses/s determined from (n-1 pulses)/duration (in seconds) measured from the beginning of the first pulse to the beginning of the last pulse]. Levels of resolution were less than 1ms for temporal aspects, and less than 40Hz for dominant frequency.

SYSTEMATICS

Family LEPTODACTYLIDAE
Subfamily MYOBATRACHINAE
Uperoleia Gray

Uperoleia altissima sp.nov.
(Figs 1-7)

MATERIAL EXAMINED

HOLOTYPE: QM J55301, an adult male collected by M. Davies, K.R. McDonald & G.F. Watson in Millstream National Park (145°22'30", 17°38'30"), altitude 820m, Atherton Tableland, NE Queensland adjacent to the park entrance, 5.2km W of Ravenshoe, on 27 January 1991.

PARATYPES: QM J19851-52, Atherton (17°16', 145°29'), I.R. Straughan; QM J19855-57, Carbeen, Atherton Mareeba Rd (17°09', 145°26'), I.R. Straughan; QM J19858, 2km S of Mareeba (17°02', 145°02'), I.R. Straughan; QM J51780-4 (formerly QNPWS N15767-15771) Windsor Tableland (16°13'30", 144°58'30'), altitude 1160-1200m, K.R. McDonald, 16 January 1989; SAM R40144-46, KU 220086 same data as holotype; SAM R40147 (formerly QNPWS N58829) Blunder Ck, Wooroora, Atherton Tableland (145°26', 17°44'), J.W. Winter, 16 June 1987; AMNH 135814 (formerly QNPWS N58823) same data, 17 June 1987; SAM R34321 Western Distributer, Windsor Tableland (145°02', 16°15'), M.P. Trenerry & G. Werren, 11 January 1989; SAM R34318 Millstream, Atherton Tableland, M.P. Trenerry & G. Werren, 15 January 1989; SAM R 34319 nr Ravenshoe, Atherton Tableland, M. Trenerry & G. Werren, 15 January 1989.

REFERRED MATERIAL: QM J31550-31553, nr Atherton, C. Corben.

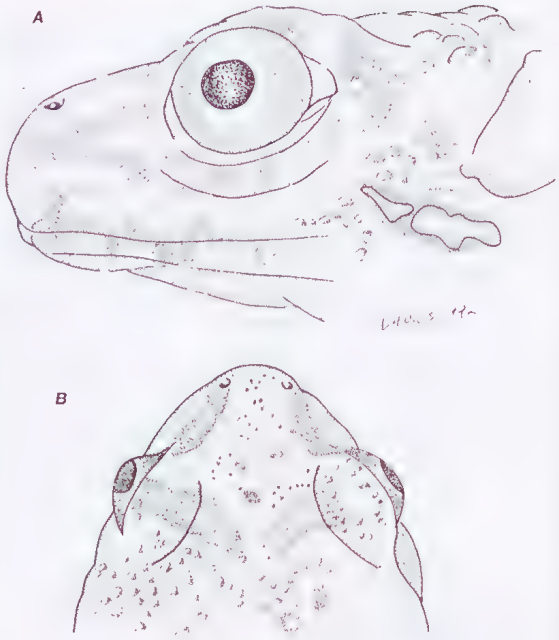

FIG. 1. A. Lateral and B. dorsal views of *Uperoleia altissima* sp.nov. (Holotype).

DEFINITION

A small species (♂♂ 19-25mm S-V) characterised by the presence of maxillary teeth; moderately developed parotoid glands; darkly pigmented ventral surface excluding the pelvic patch ventromedially on thighs; grey dorsum with strong patterning; poorly to moderately exposed frontoparietal fontanelle; no webbing between the toes; vomerine fragments present; carpus of six elements; anteromedial processes of anterior hyale of hyoid slender; ilial crest absent; advertisement call a single pulsed note of 2-3 pulses and a pulse repetition rate of 75.5 pulses/s.

DESCRIPTION OF HOLOTYPE

Maxillary teeth present. Vomerine teeth absent. Snout moderately short, slightly rounded when viewed from above, rounded in profile (Figs 1,2). Eye to naris distance greater than internarial span (E-N/IN 1.29). Canthus rostralis moderately inconspicuous and straight. Nostrils dorsolateral,

FIG. 2. *Uperoleia altissima* sp.nov. in life (Holotype).

not surrounded by prominent lip. Tympanum not visible externally.

Fingers moderately long, slender, unwebbed, slightly fringed with prominent subarticular tubercles. In order of length 3>2>4>1 (Fig. 3). Outer palmar tubercle large and prominent, inner indistinct. Hind limbs moderately short (TL/S-V 0.39). Toes long, unfringed and unwebbed. In order of length 4>3>5>2>1 (Fig. 3). Metatarsal tubercles prominent; inner elongate, lying along axis of toe 1; outer rounded, acutely angled to long axis of foot. Subarticular tubercles prominent, not conical. Parotoid glands moderately developed; inguinal glands well developed; coccygeal glands not prominent; submandibular gland prominent and discrete (Fig. 1). Cloacal flap fimbriated and prominent.

Ventral surface coarsely granular. Male with unilobular submandibular vocal sac. Cream glandular nuptial pad on thumb.

Dorsum grey in preservative with apricot tipped tubercles and overlying black patterning. Black V-shaped marking between eyes and black suprascapular plicae. Limbs banded dorsally with black. Inguinal and femoral patches cream.

Ventral surface pigmented with small cream circular patches. Femoral region unpigmented (pelvic patch). Throat darkly pigmented with tiny white stipples.

In life, dorsum grey with black patterns. Dermal glands cream; eye golden. Inguinal and femoral patches flame scarlet (Smithe, 1975).

Dimensions: S-V 21.7; TL 8.4; E-N 1.8; IN 1.4; E 2.7.

VARIATION

Uperoleia altissima is a small species ranging 18.3-25.2mm S-V. The hind limbs are short (TL/S-V, mean = 0.38 (0.35-0.43) and eye to naris distance is always greater than internarial span (E-N/IN, mean =1.40 (1.1-1.82).

SAM R40144 (recorded specimen) differs from the other topotypic paratypes in that ventral pigmentation is not as dense and the dorsal pattern is not as discrete. In addition, this paratype has an abnormal third finger on the right hand, and the dorsum is more tubercular. SAM R34318, also from the type locality, also has sparse ventral pigmentation. The paratypes from near Atherton (QM J19858, J19855-56) have reacted to preserv-

TABLE 1. Characteristics of the advertisement call of an individual of *Uperoleia altissima* sp.nov. (SAM R40144) recorded on 27 January 1991, 5.2km W of Ravenshoe, NEQ. Means (with ranges of variation in parenthesis) of 20 successive calls are shown, Effective temperature at the calling site (air wet bulb) was 24°C.

No. of pulses	Duration (ms)	Pulse repetition rate (pulses/sec)	Dominant Frequency (Hz)
2.4 (2–3)	27.51 (21.90–31.30)	75.5 (69–80)	2560 (2560)

ative and are a dense uniform chocolate brown colour, masking all dorsal and ventral pigmentation. SAM R40147 has a smaller unpigmented pelvic patch which is slightly more anterior than in the other paratypes.

Differences between topotypic and Windsor Tableland material are very slight. The tips of dorsal tubercles tend to be cream rather than apricot (probably reflecting length of time in preservative). The inner palmar tubercles of most paratypes are masked by the unpigmented glandular nuptial pad, which extends around the base of the thumb. Slight fringing of the toes and minimal basal webbing between toes 2 and 3 and 3 and 4 is present in some material. Two of the Windsor Tableland paratypes, AMNH 135814 and the largest QM J19858 show greater development of the parotoid glands.

Mating Call Structure

Twenty successive calls of the recorded individual were analysed and a summary of the call characteristics is listed in Table 1. The advertisement call of *U. altissima* is a short (mean duration 25.71ms), pulsatile call (mean pulse repetition rate 75.5 pulses/s) (Fig.4).

To the ear, the call is a sharp, loud click, repeated at a rate of about 90 calls/min. Among other species of *Uperoleia* whose calls have been described, seven (*U. aspera, U. glandulosa, U. littlejohni, U. lithomoda, U. mimula, U. minima* and *U. rugosa*) produce 'click' calls (short calls of Tyler et al., 1981a) with the call of *U. mimula* (reported ranges of variation are: duration 40-90ms; dominant frequency 2600-3300Hz; no. of pulses 3-5; pulse repetition rate 56-100 pulses/s: Davies et al., 1986) being most similar to that of *U. altissima*. The calls of these two north Queensland species are very similar except in call duration were there is no overlap in ranges of variation. Based on the calls analysed by Davies et al. (1986), the call of *U. mimula* is longer than the longer three-pulsed call of *U. altissima* (range 29.7-31.3ms). It should be noted that Davies et al. (1986) calculated pulse repetition rates using the formula 1000 (number of pulses)/ duration in ms. More accurate estimates of this derived attribute are obtained from using the formula 1000(n-1) pulses/duration in ms, or, as has been used here: 1000(n-1) pulses/duration from the beginning of the first to the beginning of the last pulses in ms. The formula used here provides the best estimate, especially in situations where the pulse duration is large compared to the interpulse interval. For comparison, recalculation of pulse repetition rate of *U. altissima*, using the formula of Davies et al. (1986), gives values of 92.8 (87-101) pulses/s.

Osteology (based on SAM R40146)

Skull well ossified. Medial ossification of dorsal sphenethmoid incomplete, overlain anteriorly by posteromedial edges of nasals; ventrally extends about 1/3 length of orbit posteriorly. Prootic not fused with exoccipital; epiotic eminences prominent. Exoccipital not fused dorso- or ventromedially. Crista parotica short, stocky; confluent laterally with long unexpanded otic ramus of squamosal. Shallow groove of carotid canal posterolaterally on frontoparietals (Fig. 5). Frontoparietal fontanelle exposed anteriorly as inverted roughly triangular area, roofed medially

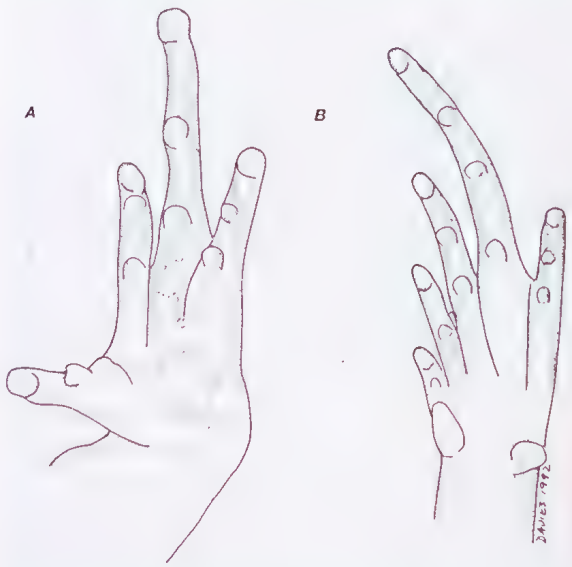

FIG. 3. A. Palmar view of hand. B. Plantar view of foot of *Uperoleia altissima* sp.nov. (Holotype).

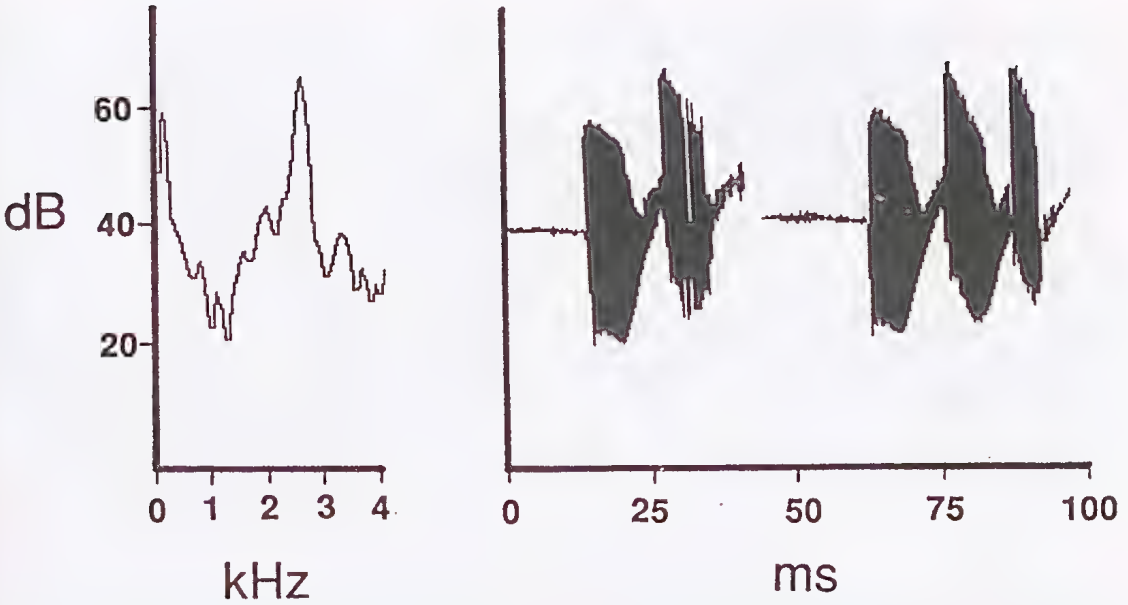

FIG. 4. Power spectrum and wave form of two advertisement calls of *Uperoleia altissima* sp.nov. (SAM R40144), recorded on 27 January 1991, 5.2km W of Ravenshoe, NEQ, at a wet bulb air temperature of 24°C. Note that the ordinate for the wave form display is not labelled because it depicts a relative linear scale in volts.

and exposed again as an approximately diamond-shaped area posteriorly. Anterior extremities of frontoparietal fontanelle about level of anterior extremities of pterygoid. Posterior extremity undefined. Frontoparietal elements well ossified reaching posterior extremities of nasals anteriorly.

Nasals well ossified, approximately triangular, closely applied medially, overlying sphenethmoid posteriorly. Maxillary process poorly developed not reaching pars facialis of maxilla. Palatines moderately broad; reduced laterally, not in contact with pars facialis of maxilla but overly sphenethmoid medially.

Parasphenoid robust. Cultriform process moderately broad, truncated terminally, not reaching level of medial extremities of palatines. Alae robust, deep, slightly angled posterolaterally reaching level of extremities of medial rami of pterygoids (Fig. 5).

Pterygoid moderately robust; slender anterior ramus in long contact with well-developed pterygoid process of maxilla. Medial ramus moderately broad, acuminate. Posterior ramus moderately broad. Small cartilaginous quadrate at articulation of base of squamosal and quadratojugal. Squamosal shaft robust; short knobbed zygomatic ramus; long unexpanded otic ramus.

Maxilla and premaxilla dentate. Teeth sparse toward pterygoid process of palatal shelf of maxilla. Teeth relatively small. Alary process of premaxilla moderately slender, not inclined posteriorly. Vomerine processes of palatal shelf of premaxilla well developed, articulating medially. Pars facialis of maxilla moderately deep posteriorly, shallower anteriorly; lacking preorbital process.

Remnant fragments of dentigerous processes of vomers medial to palatines. Bony columella extremely robust (Fig. 5).

Pectoral girdle arciferal and robust. Omosternum and xiphisternum present. Sternum cartilaginous. Left clavicle previously fractured, right slender, curved; both closely applied medially. Coracoids robust, widely separated medially. Scapula bicapitate, curved, approximately same length as clavicle. Suprascapula about one half ossified.

Eight procoelous non-imbricate presacral vertebrae. Sacral diapophyses poorly to moderately expanded. Relative widths of transverse processes: III>IV>II=V=VI>VII>VIII.

Urostyle crest about 2/3 length of urostyle. Ilium with no dorsal crest. Dorsal prominence broadly obtuse; dorsal protuberance poorly-developed dorsolaterally (Fig. 6A).

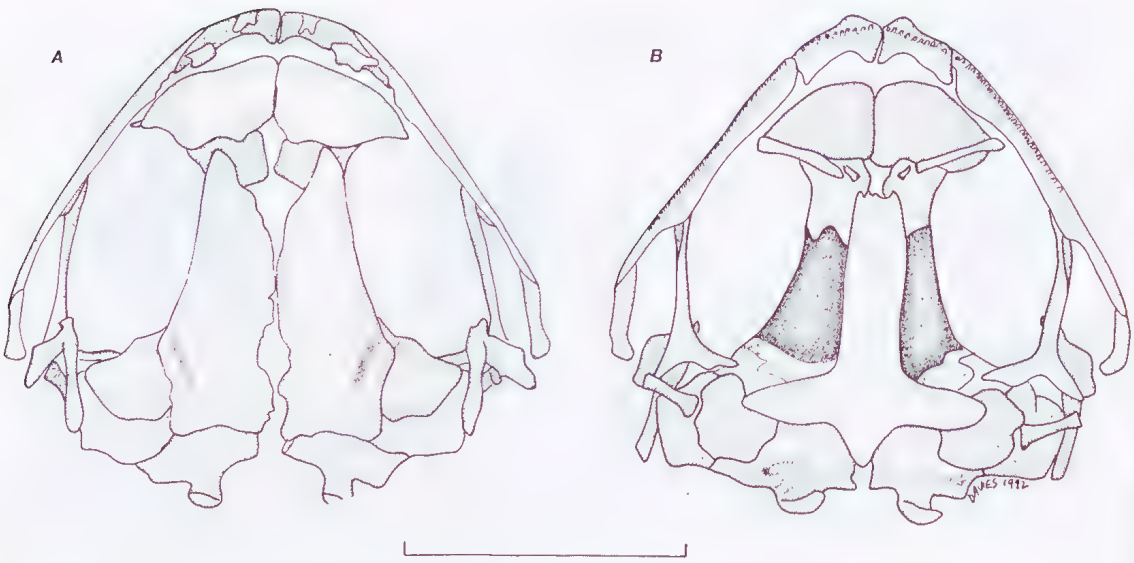

FIG. 5. A. Dorsal and B. ventral views of the skull of *Uperoleia altissima* sp.nov. (SAM R40146).

Humerus with well-developed anteroproximal crest. Phalangeal formula of hand 2,2,3,3; distal tips of terminal phalanges knobbed. Carpus of six elements, moderate torsion (Fig. 7). O. ulnare and O. radiale present. O. radiale larger of two. Both articulate with O. radioulna proximally and with each other distally. Distally both articulate with large transversely elongate O. centrale postaxiale. O. radiale articulates laterally with O. centrale preaxiale. O. centrale postaxiale articulates distally with bases of O. metacarpi III, IV and V; moderately well-developed lateral flange extends from lateroproximal corner. Palmar sesamoid anteroventrally. O. centrale preaxiale articulates laterally with O. centrale postaxiale and with unfused carpal elements of O. distale carpale 2 and 3 and laterally with basal prepollical element.

Phalangeal formula of foot 2,2,3,4,3. O. tibiale and fibulare elongated elements fused at either end. O. tibiale extends as far as distal end of O. fibulare. Three distal tarsal elements present. Lateral elements largest, lying at base of O. metatarsus III, extending laterally to articulate with medioproximal side of base of O. metatarsus IV and medially to base of O. metatarsus II. Second element lies between bases of O. metatarsi II and I. Medial element lies at the base of O. metatarsus I, articulating also with O. centrale prehallucis. Distal prepollical element subulate extending for about 2/3 length of O. metatarsus I (Fig. 7). Two sesamoids at base of prehallux.

Hyoid plate about as broad as long. Alary processes broad, not pedunculate. Anteromedial processes of anterior hyale slender and moderately long. Posterolateral processes of plate elongate. Posterior cornua long and ossified (Fig. 6B).

Variation in Osteology

Three paratypes were examined for osteological variation: QM J19581, 19587 and 51782. All are dentate but there are fewer teeth than in the described specimen. Maximum development is on the premaxilla and development decreases posteriorly. The posterior exposure of the frontoparietal fontanelle is minimal in J51782, but is the same as in the described paratype in the other two. Ossification of the nasals and of the sphenethmoid is slightly less in J51782 than that described. Development of the zygomatic ramus of the squamosal is slightly less in J19852 whilst the pars facialis of the maxilla is less crenate in J19851. Vomerine fragments are difficult to detect in this same paratype.

Etymology

The specific name is derived from the Latin *altus* meaning high, in reference to the elevations at which the species has been collected.

Comparison with other Species

Uperoleia altissima is a dentate species, a feature shared by *U. marmorata, U. mjobergi, U. micromeles, U. tyleri, U. martini, U. laevigata* and *U. fusca*.

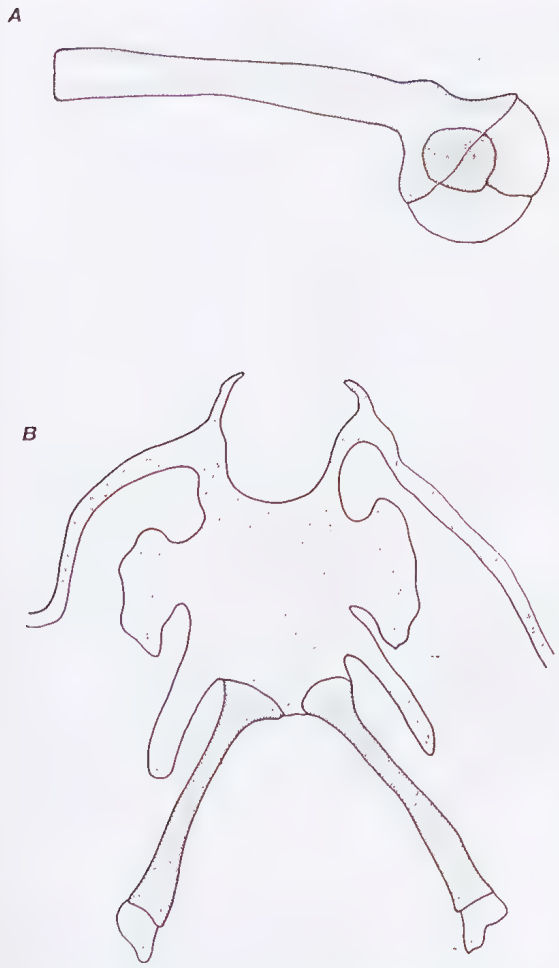

FIG. 6. A. Lateral view of the ilium (SAM R40146). B. Ventral view of the hyoid (QM J51782) of *Uperoleia altissima* sp.nov.

U. marmorata and *U. mjobergi* are confined to the Kimberley Division of Western Australia. Dentition in *U. micromeles* is sparse, similar to that found in *U. altissima*. This species is confined to desert areas in central Australia. It has very broadly spaced nasals (E-N/IN<1) and broad more elongate palatines. In addition, the shape of the nasals is unusual within *Uperoleia*. *U. tyleri* and *U. martini* are large species with hypertrophied parotoid glands and uniform ventral pigmentation. *U. altissima* is most similar morphologically to *U. laevigata* and *U. fusca*. Both these species have long calls of 32-68 or 20 pulses. In addition, both have a completely-roofed frontoparietal fontanelle and a well-developed preorbital process on the pars facialis of the maxilla.

U. altissima is most similar in call structure to *U. mimula*. This is an edentate species in which vomerine fragments are absent and which has an extremely well-developed dorsal prominence on the ilium, features not shared by *U. altissima*.

HABITAT

The type locality is medium eucalypt woodland with *Themeda triandra* and *Imperata cylindrica* (Type 16O of Tracey, 1982) and is located on Glen Gordon Volcanics. Windsor Tableland vegetation is low to medium eucalypt woodland (Type T6S) on Mareeba granites. This area was highly disturbed being near a creek system with numerous mining tracks

DISTRIBUTION

U. altissima has been located only at elevated sites on the Atherton and Windsor Tablelands, NE Queensland.

DISCUSSION

Uperoleia comprises a number of cryptic species pairs including *U. rugosa* and *U. capitulata*, *U. tyleri* and *U. martini*, *U. laevigata* and *U. fusca*, *U. inundata* and *U. arenicola*, *U. mimula* and *U. lithomoda*. The recognition of *U. altissima* adds a third example to this latter cryptic species pair.

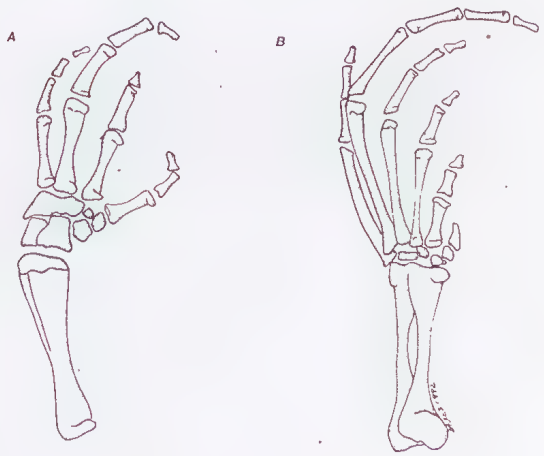

FIG. 7. A. Dorsal view of bones of hand. B. Dorsal view of bones of foot of *Uperoleia altissima* sp.nov. (SAM R40146).

Morphologically *U. mimula* and *U. lithomoda* are extremely similar (Davies et al., 1986) and close similarity in call structure between *U. mimula* and *U. altissima* exists. The presence of dentition in *U. altissima* may be the only feature that will aid field identification. Both *U. mimula* and *U. altissima* have been collected on the Windsor Tableland. The occurrence in sympatry of species with such similar call structures occurs also with *U. tyleri* and *U. martini* in southeastern Australia. To the ear on hot nights, calls of *U. mimula* and *U. lithomoda* are difficult to distinguish adding to the difficulty of field identification of this cryptic group of species.

The nature of the dentition in *U. altissima* has been shown to be a paedomorphic condition (Davies, 1989) together with a number of osteological features common to dentate species. These include the presence of vomerine fragments and the knobbed nature of the zygomatic ramus of the squamosal. Such features influenced by heterochrony provide explanations for the morphological divergences found within this enigmatic group of frogs.

ACKNOWLEDGEMENTS

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THE SPINNING FIELD AND STRIDULATING APPARATUS OF PENULTIMATE MALE *MACROGRADUNGULA MOONYA* (ARANEAE: AUSTROCHILOIDEA: GRADUNGULIDAE)

VALERIE TODD DAVIES

Davies, V.T. 1993 06 30: The spinning field and stridulating apparatus of penultimate male *Macrogradungula moonya* (Araneae: Austrochiloidea: Gradungulidae). *Memoirs of the Queensland Museum* **33**(1): 175-178. Brisbane. ISSN 079-8835.

The cribellum of penultimate ♂ *Macrogradungula moonya* is essentially bipartite but has an undivided spinning field. On the ALS there is a median cluster of about 20 major ampullate gland spigots, 2 of which are larger than the rest; on the PMS there is a single large minor ampullate spigot and 2 patches of paracribellar spigots (about 60). There is a stridulating file or ridges on the distal outerface of the chelicera and a row of 'plucking' setae arising from tubercles on the prolateral surface of the palpal femur. □ *Araneae, Austrochiloidea, Gradungulidae, spinning field, stridulating apparatus.*

Valerie Todd Davies, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 26 November, 1992.

Platnick et al.(1991) included some SEMs of the spinnerets of a juvenile *Macrogradungula moonya* in their study of haplogyne spinnerets. Apart from the possession of a cribellum and paracribellar spigots, this was shown to have greater differentiation of spigots than the ecribellate gradungulids. The penultimate ♂ (more than 20mm in body length) was expected to show this more clearly.

SPINNING FIELD

The cribellum (Figs 1,2) is narrow, six times as wide as long; the cribellar spigots are very small, close together and strobilate (Figs 3,4). The anterior spinnerets (ALS) (Figs 5,6) have a median field of about 20 major ampullate gland spigots (Map)of which 2 anterior spigots are a little larger than the rest; the ampullate spigot field is separated by a ridge from numerous piriform spigots (pi). The median spinnerets (PMS) (Figs 7,8,10) have one large minor ampullate spigot (map) with 5 aciniform spigots near its base and 11 aciniform spigots (ac) posterior to it; a large cluster of about 40 paracribellar spigots (pc) antero-medially and a further cluster of about 20 paracribellar spigots latero-distally. The posterior spinnerets (PLS) (Figs 9,11,12) have many aciniform spigots; 2 proximal spigots have wider bases than the others; tartipores (t) which are thought to be traces of spigots present in previous instars (Yu & Coddington, 1990) are present.

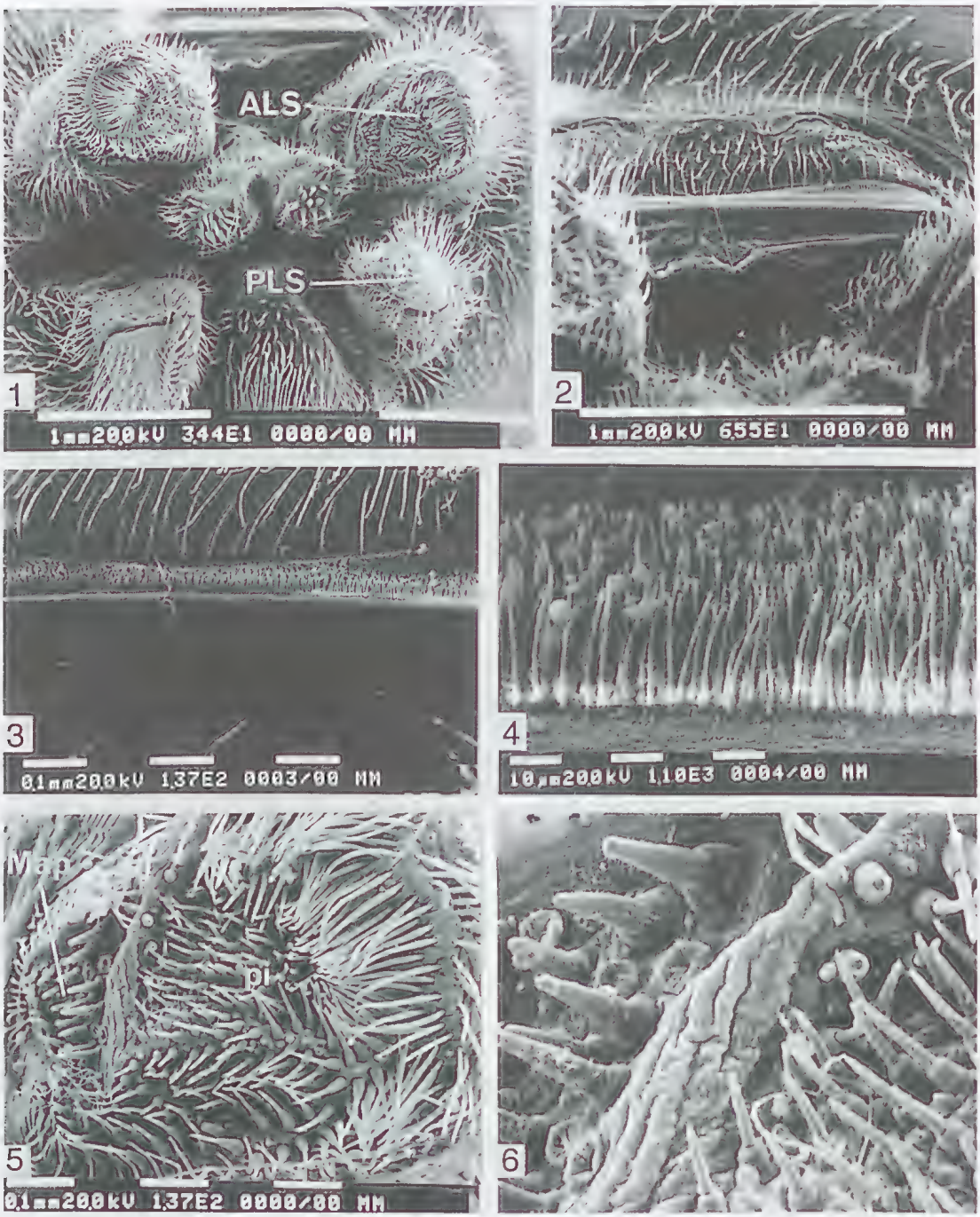
Compared with the juvenile ♀ (Platnick et al., 1991), a great increase in the number of spigots on all spinnerets is found. The bases of the paracribellar spigots are long and cylindrical, suggesting that the flat sail-like bases in the smaller spider may have been mechanically compressed to that shape.

Examination of the ♀ holotype under a light microscope revealed a similar pattern to the penultimate ♂ with an even greater number of piriform spigots on the ALS. The PMS have one large minor ampullate spigot with 2 patches of spigots (paracribellar) and a large number of aciniform spigots becoming larger proximally. The PLS have many aciniform spigots also increasing in size proximally.

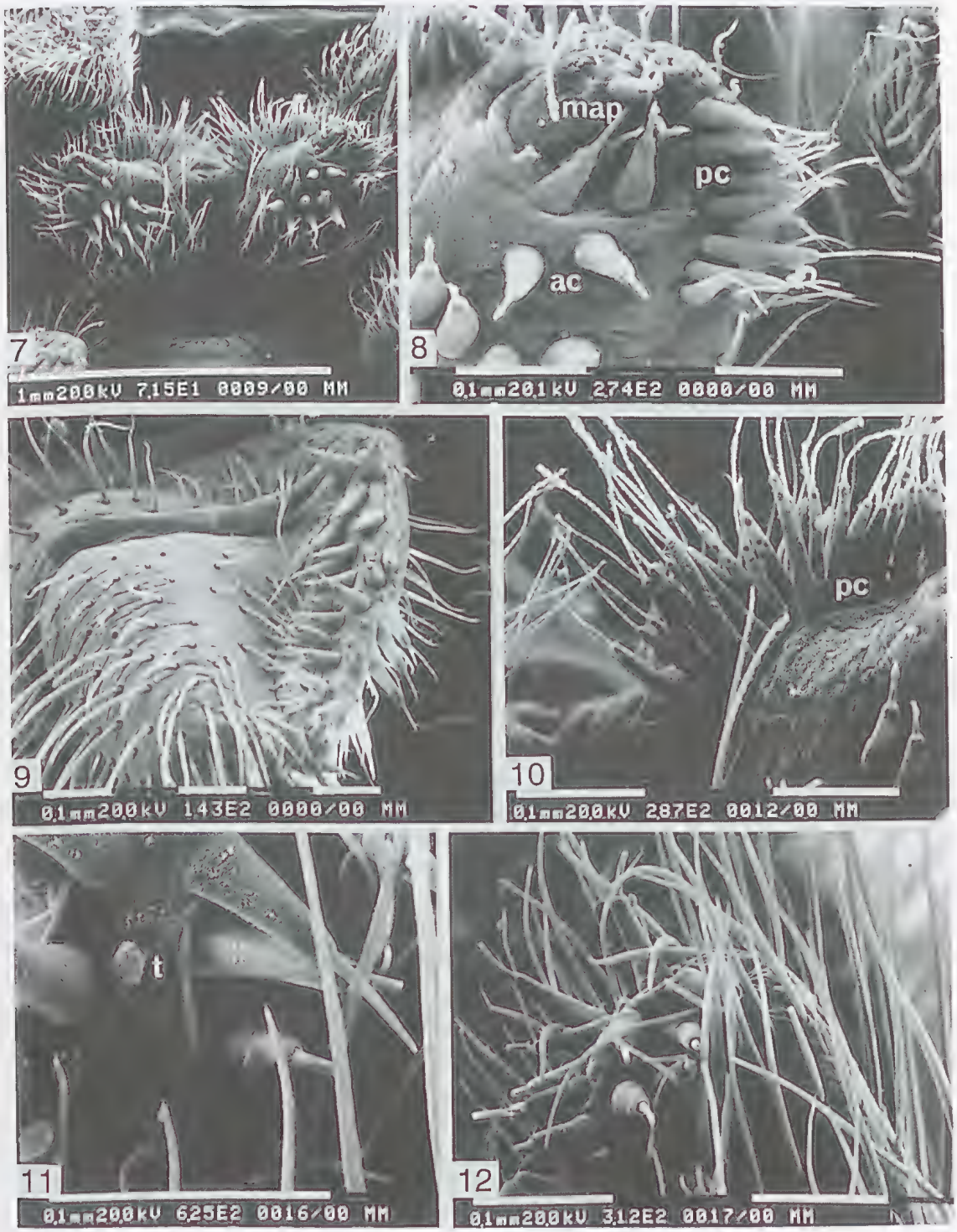
The presence of about 20 major ampullate gland spigots on the ALS is similar to that found in the hypochiloids; *Hickmania* and the South American austrochiloids have only 2 Map. Spigots on the PMS are like those in austrochiloids and have the same sculpturing pattern on the base; neither a minor ampullate spigot nor paracribellar spigots are found in the hypochiloids (Platnick et al., 1991). In the ecribellate gradungulids the minor ampullate spigot is lost along with the cribellum and paracribellar spigots.

The cribellum is homologous with the anterior median spinnerets of liphistiids and likewise the colulus when present is also homologous (Lehtinen, 1967: 398). Glatz (1972) showed that the paired muscles supplying the cribellum still persist in the colulus i.e. its bipartite history is evident. The cribellum is more than a plate of spigots; it is a movable plate supplied by muscles to each side (Glatz, loc. cit.). In the cribellum even though the cribellar field of spigots may be entire (hypochiloids and austrochiloids) the whole

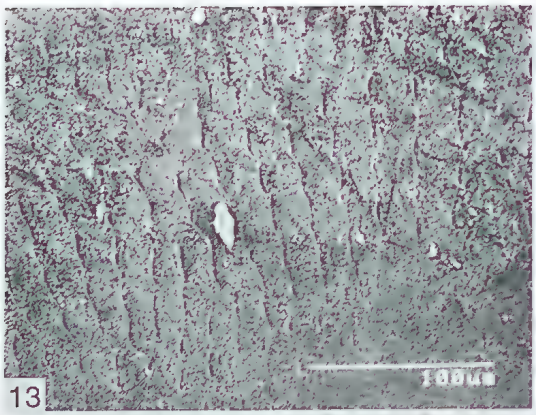
structure is essentially bipartite. This is clearly illustrated in *Macrogradungula moonya*, where the median posterior edge of the cribellum is clearly notched (Fig. 2) and the cribellar field is narrow and entire but constricted centrally (Fig. 3) suggesting that separate fields have joined.

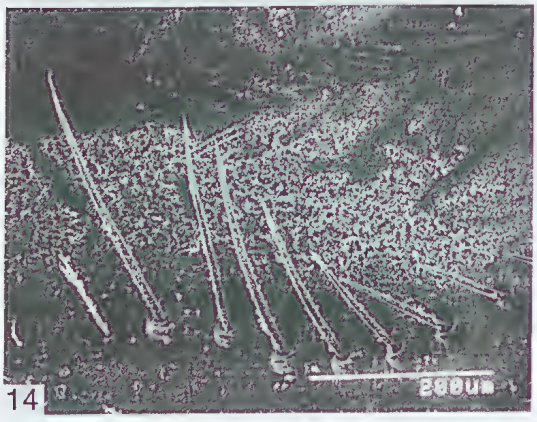


FIGS 1-6, penultimate ♂ *Macrogradungula moonya*. 1, spinning field. 2, cribellum. 3,4, cribellar spigots. 5,6, ALS, major ampullate and piriform spigots.



FIGS 7-12, penultimate ♂ *Macrogradungula moonya*. 7,8,10, PMS. 9,11,12, PLS.





FIGS 13,14, penultimate ♂ *Macrogradungula moonya* stridulatory apparatus. 13, ridged area of chelicera. 14, 'picks' on palpal femur.

Transverse serial sections of the abdomen show paired muscles from a posterior sclerite to the cribellum. Further if we consider the cribellum to be the homologue of the anterior median spinnerets and the colulus to be a functionless remnant of the cribellum then it suggests that the bipartite spinning field may be the pleisiomorphic state and the single field derived. In recent cladistic hypotheses, Platnick et al. (1991) and Coddington & Levi (1991) regard the single field as pleisiomorphic because the cribellar field of hypochiloids is entire. This single field is also found in the deinopoids, some dictynoids and some clawtufted spiders; it may have arisen more than once and is unlikely to be reversible.

STRIDULATING APPARATUS

Contrary to Gray (in Forster, Platnick & Gray, 1987: 90), a stridulatory file consisting of parallel ridges is present on a small area on the distal outerface of the chelicera, near the dorsal surface (Fig. 13). Picks in the form of enlarged setae on tubercles are found on the prolateral surface of the palpal femur (Fig. 14).

ACKNOWLEDGEMENTS

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FIRST SKULL OF A SPECIES OF *HIPPOSIDEROS (BRACHIPPOSIDEROS)* (MICROCHIROPTERA: HIPPOSIDERIDAE), FROM AUSTRALIAN MIOCENE SEDIMENTS

SUZANNE J. HAND

Hand, S.J. 1993 06 30: First skull of a species of *Hipposideros (Brachipposideros)* (Microchiroptera: Hipposideridae), from Australian Miocene sediments. *Memoirs of the Queensland Museum* 33(1): 179-192. Brisbane. ISSN 0079-8835.

Cranial material of a species of *Hipposideros (Brachipposideros)* is figured and described for the first time. The skull of the Australian Tertiary leaf-nosed bat *Brachipposideros nooraleebus* Sigé, Hand & Archer, 1982 is described on the basis of new material recovered from the type locality on Riversleigh Station, northwestern Queensland. As part of this study, morphological differences between three hipposiderids, *Hipposideros (Brachipposideros) nooraleebus, Rhinonicteris aurantius* and *Hipposideros (Hipposideros) speoris*, are reported. *Hipposideros (B.) nooraleebus* appears to be more similar to *R. aurantius* than to its congener *H. speoris*. □ *Tertiary, fossil, bat, skull, Hipposideridae, Riversleigh, Microsite.*

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In 1982, the Tertiary leaf-nosed bat *Hipposideros (Brachipposideros) nooraleebus* was described from collections made between 1976 and 1981 from the Microsite locality on Riversleigh Station, northwestern Queensland (Sigé, Hand & Archer, 1982). The Microsite deposit, which contains the Nooraleeba Local Fauna (Sigé et al., 1982), is one of more than 150 Oligo-Miocene fossil-bearing, freshwater limestone deposits on Riversleigh Station (Archer et al., 1989, 1991).

Hipposideros (Brachipposideros) nooraleebus was the first Australian Tertiary bat to be named and the first species of the subgenus *H. (Brachipposideros)* recorded from outside of France. In France, the subgenus is known from six other species also of Oligo-Miocene age (Sigé, 1968; Legendre, 1982; Sigé et al., 1982). The Australian bat was found to most closely resemble the French Burdigalian (early middle Miocene) species *H. (B.) aguilari* (Sigé et al., 1982). The appearance of closely related taxa in Australian and European sediments is enabling intercontinental biocorrelation of Australian Tertiary mammal- bearing deposits. Sigé et al. (1982) regarded *Brachipposideros nooraleebus* to be a possible ancestor of northern Australia's living endemic Orange Horseshoe Bat *Rhinonicteris aurantius*.

In 1982, *B. nooraleebus* was described, like the French *Brachipposideros* species, mainly on the basis of its teeth. By 1982, thousands of well-preserved dentaries and partial maxillae had been collected from Microsite. Subsequently, the deposit yielded partial skulls referable to this species. In this paper, cranial material of *H. (Brachipposideros)* is described for the first time and compared with the skulls of *R. aurantius* and the type species *Hipposideros speoris speoris* of India and Sri Lanka.

Dental nomenclature follows Sigé et al. (1982). Skull terminology is modified from Sigé (1966), Barghoorn (1977) and Novacek (1986, 1991). The prefix QMF refers to the fossil collections of the Queensland Museum, Brisbane. Repositories of comparative Recent specimens are indicated by prefixes as follows: M, Australian Museum, Sydney; CM, CSIRO Division of Wildlife and Ecology, Canberra; AR, temporarily held in collections at the University of New South Wales. Stratigraphic nomenclature for the Riversleigh region follows Archer et al. (1989, 1991).

SYSTEMATICS

Hipposideros (Brachipposideros) nooraleebus
Sigé, Hand & Archer, 1982
(Figs 1-4, Table 1)

Referred Specimens

QMF19034, a rostrum preserving the palate, left M^1-M^3 and alveoli for P^4 and anterior roots for left zygomatic arch (Figs 1A,2A,3); QM F19035, a braincase preserving the skull roof and basicranium with periotic bones in situ (Figs 1B,2B,3); QMF19036, a right maxillary fragment with C^1-M^3; QMF19037, a left maxillary fragment with P^4, M^1, M^3 and anterior zygomatic arch; QMF19038, a rostrum (edentulous) with

anterior zygomatic arch; QMF19039, a rostrum with right P^4-M^3 and left M^1-M^2 ; QMF19040, a left maxillary fragment with C^1-P^4 and M^2-M^3; QMF19041, a rostrum with left M^3 and anterior zygomatic arch; QMF19042, skull fragment with left P^4-M^3 and anterior dorsal cranium; QMF19043, dorsal cranium; QMF19044, ankylosed left and right premaxillae (Fig. 4); QMF19045, a right premaxilla; QMF19046, an upper I^1; QMF19047, a lower I_1; QMF19048, a lower I_2; QMF19049, posterior skull fragment preserving basicranium, glenoid surface, postglenoid process and posterior roots of zygomatic arch; QMF19050, a left periotic; QMF19051, a right periotic.

Locality, Stratigraphic Position and Age

Microsite occurs approximately 15m south of the southern end of the exposure of Carl Creek Limestone at Tedford's (1966) Site D within the Tertiary sequence of freshwater limestone sediments on Riversleigh Station, northwestern Queensland. Sigé et al. (1982) interpreted the age of the Microsite sediments, and the contained Nooraleeba Local Fauna, to be of middle Miocene age, largely on the basis of the interpreted stage of evolution of fossil marsupials preserved with the Microsite bats. The Microsite limestone was interpreted to represent a distinct facies with an uncertain stratigraphic relationship to the Carl Creek Limestone of the nearby Site D (also interpreted then to be of middle Miocene age; Archer, 1981).

Ongoing stratigraphic and biocorrelative work on the Riversleigh Tertiary limestone sequences, including study of rich mammal- bearing deposits discovered since 1983 (Archer et al., 1989, 1991) led to a reinterpretation of the age and nature of the Microsite deposit as an early Miocene cave deposit intruded into slightly older System A sediments which themselves probably date from the late Oligocene to early Miocene (Archer et al., 1989, 1991).

Associated Fauna and Taphonomy

Hipposideros (Brachipposideros) nooraleebus is represented in the Microsite deposit by tens of hundreds of individuals. It appears to be the only hipposiderid in the Nooraleeba Local Fauna, which also contains the megadermatid bat *Macroderma godthelpi* (Hand, 1985) as well as small fish, crocodiles, turtles, passerine birds, dasyurids, potoroids, a perameloid and a petauroid (Rich et al., 1991). Postcranial and dental remains of *B. nooraleebus* are commonly very well preserved in the deposit, many being complete. However, uncrushed cranial material of *B. nooraleebus* is relatively rare. Microsite fossils are particularly fragile compared with those from Riversleigh's other Oligo-Miocene bat-bearing deposits. The fossils appear to be demineralised, possibly the result of post-depositional leaching or, alternatively, a unique palaeochemistry of the depositional environment.

Diagnosis

See Sigé, Hand & Archer (1982: 152).

Description

The comments made here are intended to supplement the accompanying photographs and drawings. The skull is known from a number of

TABLE 1. Measurements of skull and upper dentition of *H. (Brachipposideros) nooraleebus*, Microsite, Riversleigh Station. L, length; w, width; d, distance. In mm.

QMF	19034	19035	19036	19037	19038	19039		19040	19041	19042
						right	left			
C^1-M^3L			5.79					5.82		
P^4-M^3L			4.34	4.40		4.36		4.30		4.56
M^1-M^3L	3.66		3.42	3.57		3.54				
P^4L			1.07	1.03		1.07		1.05		1.01
M^1L	1.34		1.40	1.46		1.35	1.47			1.45
M^2L	1.31		1.22			1.34	1.40	1.31		1.36
M^3L	1.02		0.98	1.05		0.92		0.98	1.00	1.01
PalatalL	1.63		1.77		1.47	1.69			1.77	
Interorbitalw	1.97		2.12						2.10	
Mastoidw		7.95								
Perioticw		2.88								
Interperioticd		1.43								

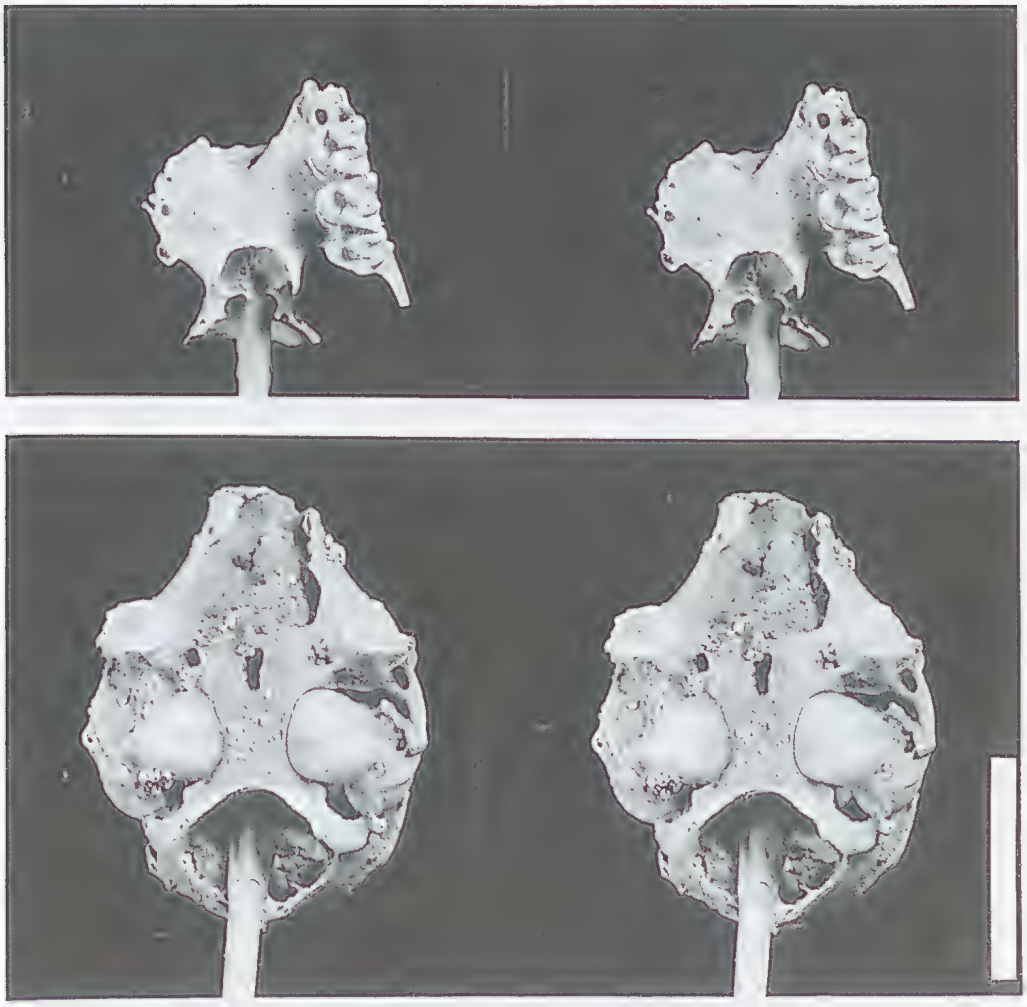

FIG. 1. *Hipposideros (Brachipposideros) nooraleebus*, Microsite, Riversleigh Station, northwestern Queensland: A, QMF19034, ventral view, stereopair; B, QMF19035, ventral view, stereopair. Bar indicates 5mm.

incomplete specimens. The most complete of these are QMF19034, a rostrum preserving the nasals, palate, anterior root for the left zygomatic arch, left M^{1-3} and alveoli for P^4, and QMF19035, a braincase preserving the skull roof, basicranial and ear regions, with periotics in place. Matrix obscures part of the right ear region but has been left in place for structural support. The description is based primarily on these two specimens but other referred specimens (see list above) provide additional information. There is no evidence of crushing of cranial material but some breakage has occurred. Some details of the medial skull region are lacking.

It has not been possible to determine the precise limits of each bone in the skull. In microchiropteran bats, sutures between bones of the skull fuse completely early in development, and no juvenile specimens of *Brachipposideros nooraleebus* have yet been recovered. However, as a guide for interpreting approximate bone boundaries in the fossil hipposiderid, several juvenile rhinolophoids were examined in this study, i.e. specimens of *Hipposideros diadema* (M20478), *Rhinolophus megaphyllus* (AR17575) and *Macroderma gigas* (M11762, M27675).

General outline and proportions. The skull is small, slender and strongly constricted in the interorbital region. The rostrum is relatively broad and long. The rostral length is approximately half the length of the braincase and its greatest width, at the level of the most anterior point of the orbit

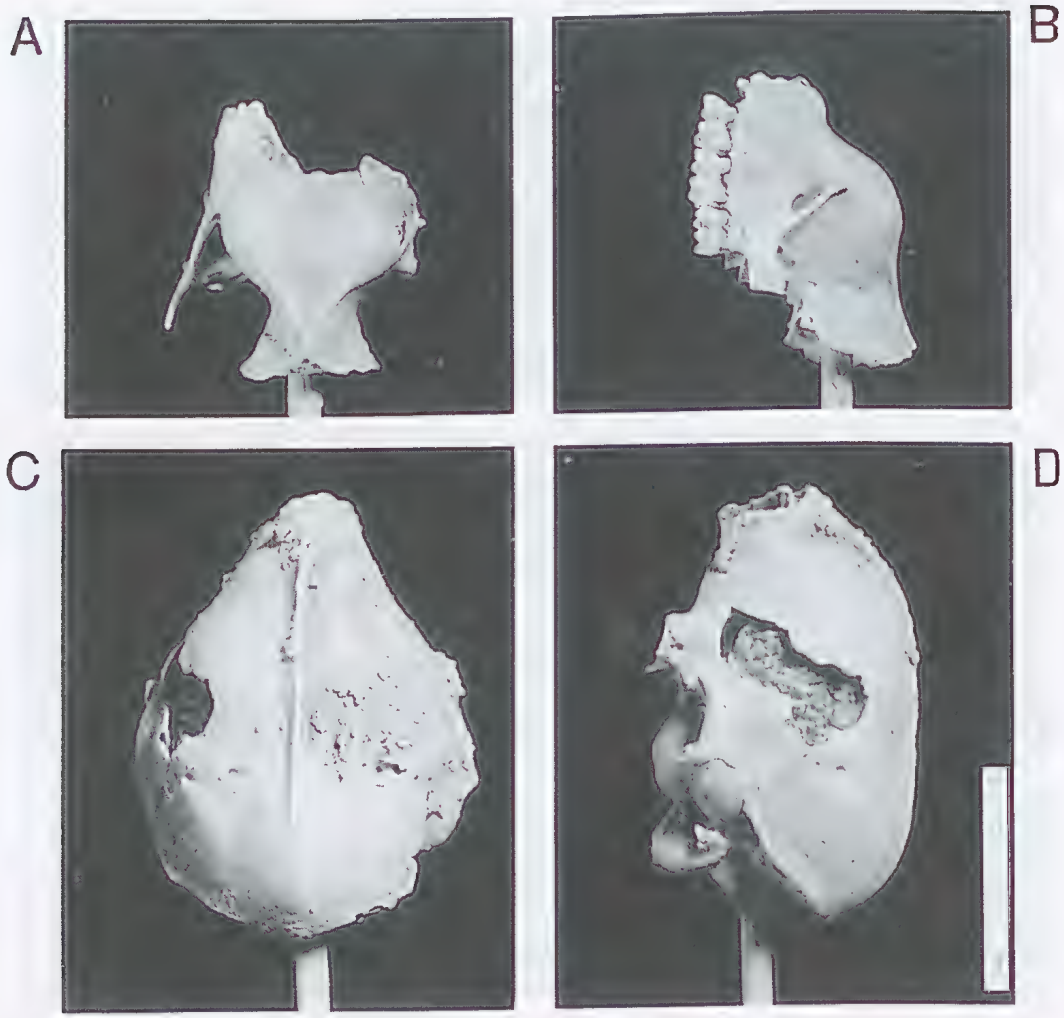

FIG. 2. *Hipposideros (Brachipposideros) nooraleebus*, Microsite, Riversleigh Station: A-B, QMF19034, dorsal and lateral views; C-D, QMF19035, dorsal and lateral views. Bar indicates 5mm.

(the lacrimal foramen), approximately two-thirds the mastoid width and more than twice the interorbital width. In height, the rostrum is lower than the braincase. The braincase is broadest across the mastoids (at the level of the post-tympanic processes). The maximum zygomatic width is not known.

Rostrum. The rostrum is square in outline, being approximately as long as wide and with subparallel lateral borders. It is deeply notched anteriorly, this indentation describing a broad arc between the maxillae. Conspicuous rostral inflations are separated by a broad, shallow trough delimited by well-developed supraorbital ridges. These are better defined posteriorly than anteriorly where they are attenuated by the nasal inflations. In the trough, at a point approximately midway between the anterior margin of the nasals and the junction of the supraorbital ridges, is a small, unpaired foramen. The rostral inflations are most conspicuous in lateral view, such that in profile the face is not gently inclined but rises almost vertically from the level of the palate to the maximum height of the rostrum.

The zygomatic arch extends onto the face as a very thin arch that joins the lateral wall of the maxilla. Under this arch (i.e. enclosed by a narrow bar of bone) opens the anteroposteriorly elongated infraorbital foramen. Hidden in lateral view by the arch, two orifices open in the lateral

wall of the face at the front of the orbital fossa. The first, the lacrimal foramen, opens under the anterior attachment point of the arch at the edge of the circumorbital rim, and is separated from the infraorbital foramen by only a thin wall of bone. Posteriorly, at the ventral part of the anterior recess of the orbital fossa, is the second orifice: a broad, deep fossa that exposes the maxillary bone covering the roots of the posterior cheekteeth. Medial to this, at the most anteroventral point of the orbit, is a post-palatal foramen which leads through into the palate. More posterodorsal and medially, in the lateral wall of the interorbital constriction, two small foramina open into a long, curved, shallow groove that leads posterodorsally from the post-palatal foramen to the optic foramen. Dorsal and medial again in the interorbital region is a deeper, shorter, anteroposteriorly directed sinus into which a number of foramina also open at the level of, or just posterior to, the cribriform plate of the ethmoid. These foramina appear to vary in number, form and position (and from one side of the skull to the other) perhaps varying epigenetically.

Palate. The palate is short. The toothrows are not convergent anteriorly. At the palate's anterior edge is a deep, V-shaped indentation, which extends posteriorly to the level of the posterior face of M^1, for the junction with the premaxillae. The palate's posterior border has two deep posterolateral indentations that extend anteriorly to at least the level of the anterior face of M^3. Each closely skirts M^3 and forms a recess beside the palatine. The posterior extension of the midline of the palate is level with the anterior face of M^3; a medial palatal spine is variably developed. The maximum width of the palate is at the level of M^2. The palate is almost flat though slightly concave longitudinally. The most constant and well developed palatal foramina are medial to the anterior face of M^1. Other foramina appear to be variable but a fossa medial to M^{2-3} is usually perforated by a number of foramina and on the midline, medial to the posterior face of M^1, an unpaired foramen occurs in some specimens.

Premaxillae. The ankylosed premaxillae comprise a small, loose element that bears a single pair of incisors. The best preserved specimens are QMF19044 (Fig. 4) and QMF19045 but the incisors have been lost from both. The premaxillae gently flare anteriorly. The incisor alveoli occur at the anterior edge in a medial position. Posteriorly, two thin premaxillary processes probably do not fully enclose large anterior palatal foramina. The premaxillae are very thick with, at their line of contact, a distinct crest on the dorsal surface. The dorsal surface is convex in both horizontal and longitudinal axes. In anterior view, the convexity is rather gentle. In lateral view, it is more acute and is accentuated by the distinct posteriorly directed crest. This reaches its maximum height about one-third the distance from the premaxillae's anterior edge. The incisors would have been directed ventrally. The ventral surface of the premaxillae is generally gently concave longitudinally but posteriorly it is domed.

Nasals. The inflated nasal cavities are bilaterally symmetric, being divided by a median septum. The dorsal border of the septum parallels the palate rather than the contour of the face. Posteriorly, the septum fuses with the anteriorly inclined cribriform plate. The posterior face of the plate is deeply concave and perforated by many foramina of varying sizes. The endocranial space is arched over the inclined cribriform plate. Posteriorly, curved lateroventral extensions of the median septum (subethmoidal shelves) partially separate each nasal cavity into a ventromedial respiratory section and more extensive dorsal and lateral olfactory sections. The latter are further subdivided, by a thin ethmoidal lattice, into anterior and posterior chambers. The ethmoturbinal mass appears to have been very simple but is not well enough preserved to be confidently described. Above the cribriform plate, the nasal cavity expands into a broad chamber roofed by the frontals.

Interorbital and pterygoid region. Immediately to the rear of the face and between the orbital fossae, the braincase narrows. The point at which the two supraorbital crests unite (i.e. where the sagittal crest originates) is clearly posterior to the point of narrowest constriction. The pterygoid wing, sloping ventrally and laterally, forms the posteromedial wall of the orbital fossa. The side wall of the skull is pinched in between the cranium and the palatine and pterygoid wings, and hence the optic foramen and sphenorbital fissure open ventrally from the braincase. The sphenorbital fissure was evidently long and wide, a very narrow bony bridge separating it from the large, almost semicircular optic foramen. Immediately lateral to the most anterolateral margin of the sphenorbital fissure is a small, round foramen. Anterior to the optic foramen is the cribriform plate of the ethmoid. Small pterygoid processes occur at a point laterally in line with the junction of the supraorbital ridges and posterior to M^3 at a distance approximately equal to the length of M^3. If hammular processes were present they are now

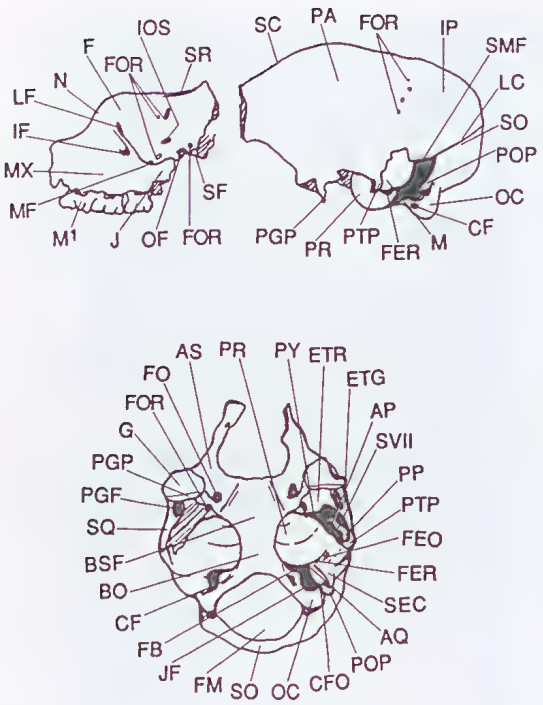

FIG. 3. *Hipposideros (Brachipposideros) nooraleebus*, Microsite, Riversleigh Station. Top, QMF19034 and QMF19035, lateral views. Bottom, QMF19035, ventral view. AP anterior process; AQ aqueductus cochleae; AS alisphenoid; BO basioccipital; BSF basisphenoid fossa; CF condyloid foramen; CFO condyloid fossa; DC dorsal crest; ETG epitympanic groove; ETR epitympanic recess; F frontal; FB basicochlear fissure; FEO oval window; FER round window; FM foramen magnum; FO foramen ovale; FOR foramen; G glenoid; IA incisor alveolus; IF infraorbital foramen; IOS interorbital sinus; IP interparietal; J jugal; JF jugular foramen; LC lambdoidal crest; LF lacrimal foramen; M mastoid; M^1 first molar; MF maxillary fossa; MX maxilla; N nasal; OC occipital condyle; OF optic foramen; P periotic; PA parietal; PGF postglenoid foramen; PGP postglenoid process; PL palatine; PM premaxilla; PMP premaxillary process; POP paroccipital process; PP posterior process; PR promontorium; PS presphenoid; PT pterygoid; PTP post-tympanic process; PY pyriform fenestra; SC sagittal crest; SEC semicircular canals; SF sphenorbital fissure; SMF supramastoid foramen; SO supraoccipital; SQ squamosal; SR supraorbital ridge; SVII sulcus for facial nerve (VII). Bar indicates 5mm.

missing. The posterior edge of the pterygoid wing curves ventrally and posteriorly and slightly medially before forming a second, laterally-directed flange.

Zygomatic arch. The ventral margin of the zygomatic arch is slightly arched and lies dorsal to the tooth row. Anteriorly, the dorsal margin sinks in the jugal region then, posteriorly, rises at an angle of approximately 45 degrees to the ventral surface to form the very tall squamosal projection. The latter rises to at least the level of the dorsal edge of the infraorbital foramen. Its maximum height occurs dorsal to the glenoid surface. A masseteric scar occurs on the anterolateral ventral surface of the arch. In dorsal view, the junction between the zygomatic arch and its anterior extension onto the face is marked by a change in direction of the arch from posterolateral (anteriorly) to posterior, the anterior extensions diverging far more than the zygomatic arches proper. The latter appear to have been almost parallel for much of their length.

Cranial vault. The braincase is widest at the level of the post-tympanic processes, narrowest in the interorbital area and highest dorsal to the postglenoid processes. There is little development of the lambdoidal crests and no nuchal crest so that the braincase is rounded at its posterior extremity in lateral and dorsal views. The sagittal crest is variably developed (perhaps reflecting sexual dimorphism). Where it occurs, the sagittal crest is low and extends anteriorly to the supraorbital ridges and posteriorly to the interparietal at a point dorsal to the paroccipital processes. Approximately two-thirds along the length of the braincase, within the parietals, are bilaterally depressed areas that mark a conspicuous venous sinus. Its trajectory is easily traced in a lateral then anterolateral direction before it opens to the exterior in the posterior part of the postglenoid foramen. Along the sinus several small orifices open to the exterior.

Glenoid. The glenoid surface is only slightly concave and is subcircular, being almost as long as wide. It ends medial to the zygomatic process of the squamosal. The postglenoid process is weak. In height it is less than one quarter the length of the glenoid surface; its anterior face is not noticeably anteriorly recurved. The large postglenoid foramen opens vertically on the steeply sloping posterior face of the glenoid, giving the opening an elliptical shape. It opens immediately posterior to the postglenoid process. Medial to the glenoid surface, the foramen ovale opens in the alisphenoid on the side of a bony prominence or ridge. The latter separates the ventrally opening foramen ovale from a second, more posterodorsal and lateral foramen that opens posterolaterally (i.e. into the pyriform fenestra).

Temporal region. Posterior to the glenoid region and immediately anterior to the mastoid

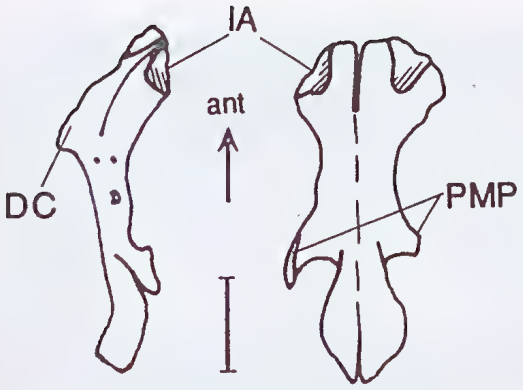

FIG. 4. *Hipposideros (Brachipposideros) nooraleebus*, Microsite, Riversleigh Station. QMF19044, left ventral view; right lateral view. Bar indicates 1mm.

region, the post-tympanic process of the squamosal is developed with a vertical process that forms a slim posteromedially directed point. In lateral view, the posteroventral part of the lateral face of the periotic is exposed and the round window visible. In the otic region, the squamosal swells slightly laterally and circumscribes an indentation which would have accommodated the tympanic ring. The squamosal laterally and anterolaterally, the alisphenoid anteriorly and the basisphenoid medially, contribute to the anterior edge of the cavity occupied by the periotic. At the anterolateral corner of the tympanic cavity, the pyriform fenestra forms a broad gap separating the posterior face of the glenoid from the anterolateral wall of the periotic. The posterolateral wall of the skull is deeply notched between the post-tympanic process of the squamosal and the paroccipital process. This notch is filled by the mastoid.

Basicranium. The medial sphenoid series (basisphenoid and presphenoid) is broadly fused with the palatine, pterygoid, alisphenoid and basioccipital. The basisphenoid appears relatively flat in its central region or perhaps only slightly concave. Faint, anteriorly convergent ridges define the basisphenoid fossa (and mark the boundary between the pterygoid and basisphenoid anteriorly and probably the alisphenoid and basisphenoid posteriorly). The periotics are not enlarged, their width being about twice the shortest distance between the two. Thus the lateral edges of the basisphenoid-basioccipital complex are relatively straight with only shallow biconcave lateral curves. The anterior margin of the basicranial area is not preserved. The periotic is bordered medially and posteriorly by the basioccipital. Anteromedially, the basisphenoid abuts the periotic; there is no lateral extension of the basisphenoid or medial extension of the petrosal.

Occipital. The most posterior region of the skull coincides with the junction of the interparietal and supraoccipitals. In lateral view, the supraoccipital is not very convex posteriorly but the exoccipitals nonetheless overhang the posteroventrally directed foramen magnum. The posterior edge of the foramen magnum is straight and not thickened. There is little development of the lambdoidal crests but a distinct ridge marks the junction of the interparietal and supraoccipitals. It parallels the posterior edge of the foramen magnum, terminating anteriorly in the region dorsal and lateral to the paroccipital process, i.e. immediately to the rear of the mastoid region. A supramastoid foramen opens on the occipital surface dorsal to the ventral condyloid fossa. There are no parietal crests and no posteriorly directed point on the skull: the nuchal line continues smoothly over the top of the skull.

In ventral view, the posterior skull contour of the supraoccipital at the level of the lambdoidal ridge is rounded. The foramen magnum is oval in shape and wider than high. Between the occipital condyle and paroccipital process is a deep condyloid fossa. The paroccipital process is well developed and forms the lateral-most part of the occipital bone. The tip is not preserved but the process appears to have articulated with the mastoid. The condyle projects most strongly ventrally at the posterior extremity, its thickened lip partially concealing the condyloid foramen in the anterolateral face.

Ear region. The ectotympanics and auditory ossicles are missing. The periotic is only weakly articulated with the surrounding basicranial elements and exhibits the condition described by Novacek (1991) as 'phanerocochlear' found in most adult microchiropterans. In this species, attachment of the periotic appears to be solely via connective tissue although the periotic closely abuts the basicranial elements medially via the basisphenoid-occipital complex and laterally via the post- tympanic process of the squamosal and the paroccipital process. The anterior part of the middle ear cavity is unossified as a pyriform fenestra which is a restricted opening between the periotic and the squamosal and most posterolateral part of the alisphenoid. There is little development of an epitympanic recess or ectotympanic groove, the bone here being no thicker than the squamosal that bounds it. Posteriorly, the large

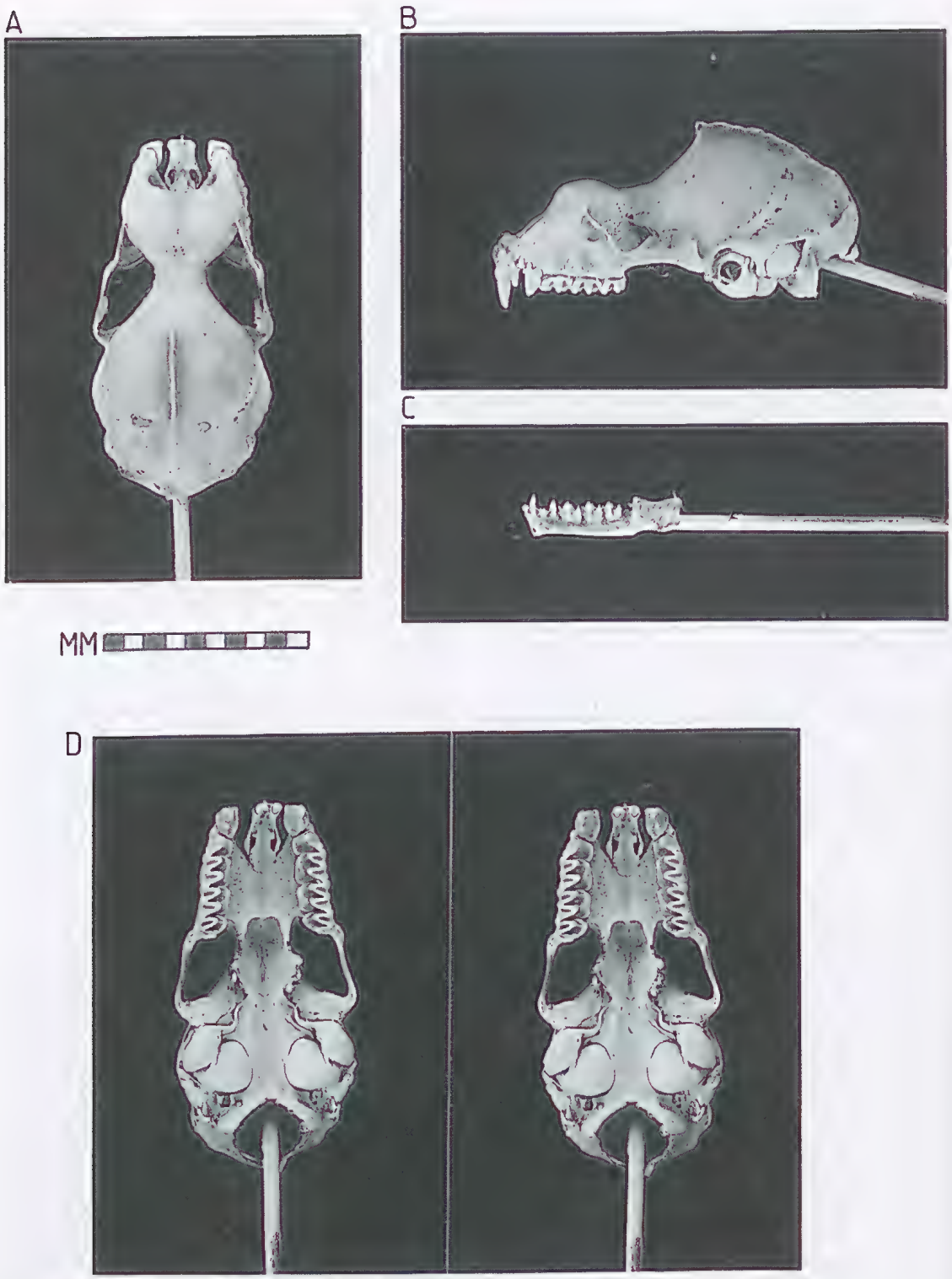

FIG. 5. *Rhinonicteris aurantius*, AR15400, Klondyke Queen Mine, Marble Bar, Western Australia. A, skull dorsal view; B, skull lateral view; C, jaw lateral view; D, skull ventral view, stereopair. Scale in mm.

jugular foramen and the more medial, very narrow basicochlear fissure are coalescent.

In ventral view, the cochlear labyrinth is visible through the thin bone of the promontorium so that the petrosal has a snail- like appearance. Three turns of the labyrinth can be detected through the bone and this is confirmed by examination of sectioned periotics.

In the lateral face of the periotic the following structures are visible. Most posteriorly, above the ventral plane of the basioccipital and facing the jugular foramen, is the aqueductus cochleae. Lateral and ventral to this, at the posterolateral corner of the periotic and distinct in ventral view, is the round window, a large, flattened oval orifice. More anteriorly and dorsally, the oval window is slightly more elongate. A very slight transverse groove, barely imprinted on the promontorium medial to the round and oval windows, marks the passage of the stapedial artery, a branch of the internal carotid. Lateral to the round and oval windows, and at the base of the promontorium, is a deep, elongate, curved depression or canal which dips from front to rear. This is the canal for the facial nerve (VII). The canal terminates posteriorly a little anterior to the round window in the region of the stapedial fossa and continues anteriorly beyond the oval window via an orifice (the apertura tympanica canalis facialis).

The lateral margin of the canal is a vertical, curved face. Anteriorly, a small process (the anterior process of the petrosal; Henson, 1970) protrudes anteromedially into the pyriform fenestra. It does not articulate with the squamosal. Near its base is a small foramen (possibly for the superior ramus of the stapedial artery). Behind this process the lateral edge of the periotic curves back and dorsal and is appressed closely to the squamosal. Immediately medial to the post-tympanic process, the lateral edge terminates in a prominent process (posterior process of the petrosal; Henson, 1970) that overhangs the stapedial fossa.

The mastoid occupies a lateral, posterior and dorsal position in the periotic. The mastoid wall only thinly covers the three semicircular canals.

Incisors. The dentition of *B. nooraleebus* has been described previously by Sigé et al. (1982), except for the incisors which are now known as follows. There is one pair of upper incisors, I^1, and two pairs of lower incisors, $I_{1\text{-}2}$. The upper incisors are bilobed with the outer lobe slightly wider but shorter than the inner lobe. The lower incisors are tricuspidate and I_1 is smaller than I_2.

COMPARISONS

RHINONICTERIS AURANTIUS

The skull of *B. nooraleebus* is smaller than that of *R. aurantius* (Gray, 1847) (AR17573, M8416, AR15400; Fig. 5) being approximately three quarters its size. Its shape is generally similar but differs as follows. The rostrum is lower in *R. aurantius* and has less prominent inflations. The trough separating the rostral inflations is deeper and narrower, poorly delimited by supraorbital ridges and is perforated by tiny foramina. The bar of bone that extends the zygomatic arch anteriorly onto the face, and encloses the infraorbital foramen, is directed dorsally (i.e. vertically) then anterodorsally so that it appears much more convex.

The postpalatal foramen is much smaller in *R. aurantius* and is surrounded by many small foramina. Dorsal and medial to this, there is one foramen (rather than two) opening into a groove. In general, unlike *B. nooraleebus*, the skull of *Rhinonicteris* is perforated by many tiny foramina, particularly in the interorbital and pterygoid regions. The palates are similar. The premaxillae are strikingly similar except that in *R. aurantius* the anterior premaxillary processes completely enclose the anterior palatal foramina. The premaxillae of both taxa exhibit a very distinctive dorsal crest as well as a dorsal convexity that results in the incisors being directed ventrally rather than anteriorly.

The sagittal crest is quite different. In *R. aurantius* it is tall and originates abruptly (with an anteriorly curved point) at the highest point of the skull (i.e. dorsal to the postglenoid process) and does not extend as far posteriorly. The vertical projection of the zygomatic arch is possibly taller and extends further anteriorly, involving the jugal and hence most of the zygomatic length. The lambdoidal crests are better developed (especially laterally) giving the posterior margin of the braincase a squared rather than rounded appearance. The postglenoid process is better developed (being more curved) and the pterygoid region less constricted. Ridges defining the basisphenoid fossa are weak and almost parallel (rather than convergent). The postglenoid foramen is elliptical and proportionately smaller. The dorsal margin of the foramen magnum is indented.

The ear region is very similar in the two taxa. The general orientation and attachment of the periotic to surrounding basicranial elements is similar and periotic morphology very similar. In the periotic the bony wing developed lateral to the

anterior and posterior processes is not as well developed.

As described by Sigé et al. (1982), C^1 of *R. aurantius* has a better developed secondary cusp and less developed cingulum, and there is more expansion of the heel on M^2. The dentaries are similar. In both taxa the horizontal ramus is short and slender with a chin process, the coronoid process is very low (the tip only exceeding the molar heights by a molar crown height or less) and the masseteric fossa has a very expanded, almost horizontal border which extends posteriorly into a wide, rounded angular process that is buccally markedly extended.

HIPPOSIDEROS (HIPPOSIDEROS) SPEORIS

The skull of *H. speoris* (Schneider, 1800) (M3468; Fig. 6) is described in so far as it differs from both *B. nooraleebus* and *R. aurantius* except where specifically stated. It is similar in size to *R. aurantius* and approximately one-third larger than *B. nooraleebus*. The rostrum is proportionately narrower, the braincase wider and the rostral inflations, and trough separating them, less conspicuous. The posterior trough is also shallower. The supraorbital ridges are much better defined laterally (being less attenuated by inflations). The facial portion of the skull slopes posterodorsally more gradually. The bar of bone anteriorly extending the zygomatic arch onto the face is directed anterodorsally and is straight (or even concave) rather than convex. The infraorbital foramen occurs above M^1 rather than M^2 and is lower on the face. The lacrimal foramen is larger (than in *R. aurantius* at least) and the ventral fossa much broader and alveolar foramina more conspicuous than in *B. nooraleebus* and *R. aurantius*. More of the lateral face is visible (i.e. the bar of bone hides less) and a third foramen, occurring dorsal and posterior to the lacrimal, is visible on the lateral wall of the rostrum.

There appear to be two foramina posterior to the palate (the more lateral one perhaps being homologous to the postpalatal foramen observed in *B. nooraleebus). Unlike B. nooraleebus* but like *R. aurantius*, the skull is perforated by many tiny foramina especially in the interorbital region, where, for example, many open into the interorbital sinus. Note that although the sinus is present in the three taxa examined it has a different form in each. The sphenoidal fissure is relatively shorter perhaps because the skull proportions differ. Compared to *R. aurantius*, the braincase of *H. speoris* is relatively longer and the interorbital region shorter.

The palate differs in that the toothrows are anteriorly convergent, the posterolateral indentations extend to the the posterior faces of M^2 and the posteromedial palate is marked by an indentation rather than a spine. There are many tiny palatal foramina but most pronounced are a pair of foramina medial to the anterior faces of M^2 and the anterior limits of the lateral indentations (i.e. medial to the posterior faces of M^2). In the premaxillae, the processes only partially enclose the anterior palatal foramina (these processes appear to diverge posteriorly), there is no dorsal crest, little lateral convexity and the incisors are directed anteriorly. The supraorbital ridges unite at the level of the narrowest constriction in the interorbital region rather than posterior to it.

The pterygoids are more constricted and there is no second flange on the pterygoid wing. The squamosal projection of the zygoma is much less well developed. In *H. speoris* it rises from approximately halfway along the zygomatic arch to quickly reach its maximum height (level with the dorsal margin of the ectotympanic ring). In *R. aurantius* it arises further anteriorly, so that its development involves almost the entire length of the zygomatic arch, to more gradually reach at least twice this height. (Note that there may be some variation in the height and shape of this projection in *R. aurantius*: cf. AR15400 and AR17573.) In both, however, the maximum height of the projection is reached at a point above the glenoid surface. In *R. aurantius* the projection leans dorsomedially towards the braincase; it is vertical in *H. speoris*.

The braincase narrows immediately anterior to the post-tympanic process rather than anterior to the postglenoid process. Like *B. nooraleebus* but unlike *R. aurantius*, there is little development of the lambdoidal crests so that the posterior margin of the skull appears rounded. The sagittal crest is similar to *B. nooraleebus* but the latter extends further posteriorly. The postglenoid process is better developed than in *B. nooraleebus* and *R. aurantius*. The articulating surface is wider; it is oval rather than subcircular. The postglenoid foramen is small and circular rather than large and oval. Dorsally and posteriorly are a number of tiny foramina which vary in number, size and position from one side of the skull to the other.

Medial to the glenoid surface are a number of foramina, the largest and most medial presumably being the foramen ovale. The sphenoid complex is concave rather than flat and the lateral margins of the basisphenoid-occipital more concave than in *B. nooraleebus* and much more so

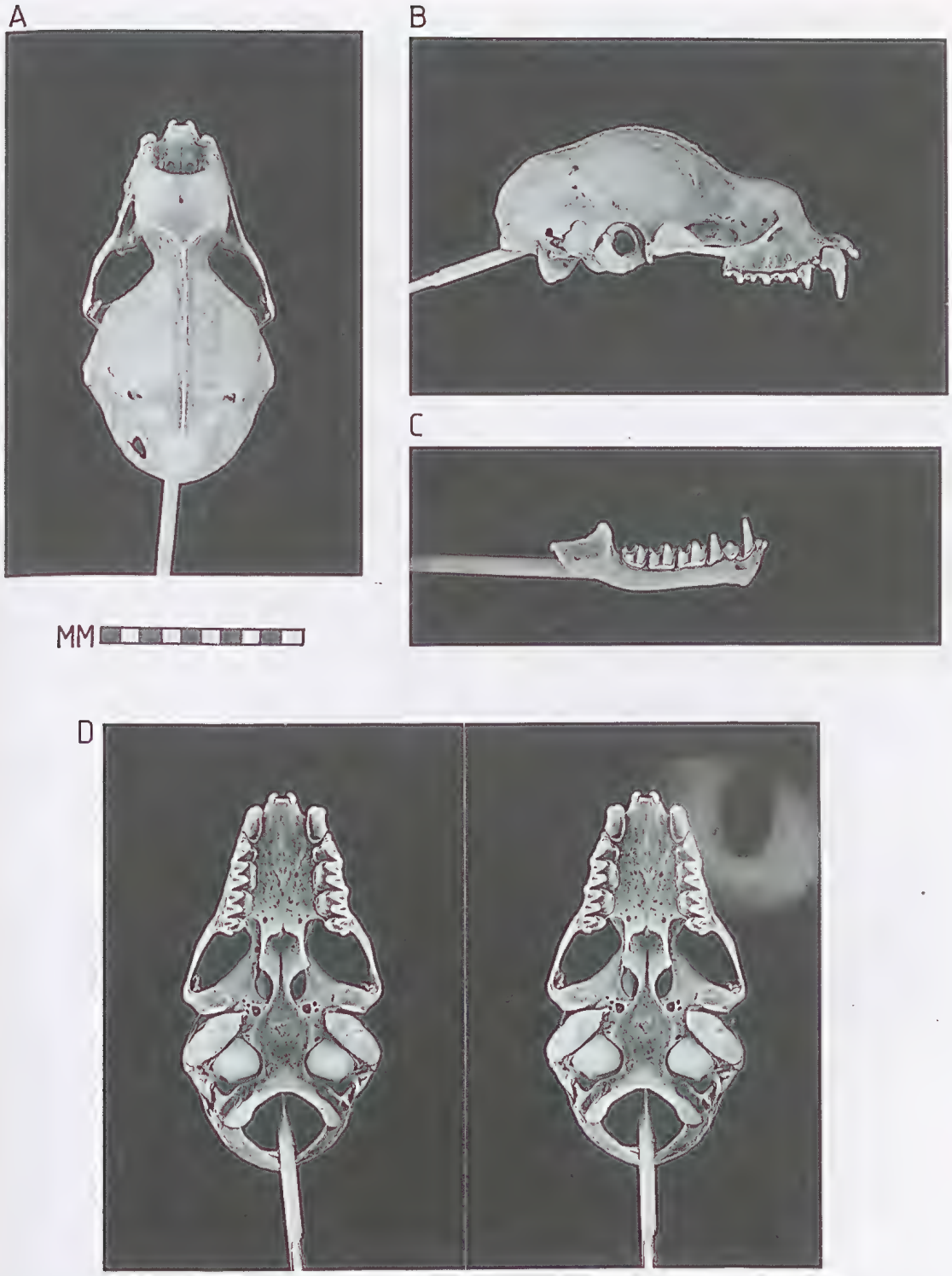

FIG. 6. *Hipposideros speoris speoris*, M3468, Kalutara, Sri Lanka. A, skull dorsal view; B, skull lateral view; C, jaw lateral view; D, skull ventral view, stereopair. Scale in mm.

than in *R. aurantius*. There is a lateral extension of the basisphenoid over the anteromedial corner of the periotic and foramina occur at the the most lateral point of the extension. As in *B. nooraleebus*, the dorsal margin of the foramen magnum is straight. The foramen magnum is oval, being conspicuously wider than long. The junction of the interparietal and supraoccipitals terminates laterally at the paroccipital process (rather than dorsolateral to it). Differentiation of the jugular foramen and basicochlear fissure is less conspicuous (i.e. their coalescence is more gradual) due to the different shape of the occipital (i.e. its lack of an extra wing). The paroccipital process articulates with the mastoid and squamosal. The notch between the paroccipital process and post-tympanic process is shallower (i.e. is filled in more posterodorsally by the squamosal and the supramastoid foramen is round rather than triangular in lateral view.

Attachment of the periotic to surrounding basicranial elements differs. The periotic abuts the basisphenoid anteromedially rather than medially and the basisphenoid extends onto the anterior promontorium. The basicochlear fissure is located medially and posteromedially and is much larger and more coalescent with the jugular foramen. The anterolateral face of the periotic is flattened. The anterior process of the periotic probably abuts the squamosal which contributes to the better- developed epitympanic recess. The pyriform fenestra appears to be narrower.

In *H. speoris*, I^1 has a reduced outer lobe, C^1 has a less developed secondary cusp and cingulum, P^2 is slightly less buccally extruded from the tooth row than in *B. nooraleebus*, M^2 heel less expanded, and M^3 more reduced such that it is narrower and shorter and the premetacrista is shorter. The coronoid process of the dentary is not as low and the angular process is narrower and extends more posterobuccally than buccally. The lower incisors protrude anteriorly, C_1 is relatively tall, P_2 small and M_3 more reduced (shorter and narrower but with a hypoconulid).

DISCUSSION

The Old World tropical to subtropical bat family Hipposideridae contains sixty-plus living species referred to the genus *Hipposideros* (approximately 50 species) and eight other genera (of one to two species each) including *Rhinonicteris*, *Coelops*, *Triaenops*, *Cloeotis*, *Asellia* and *Aselliscus* (Hill & Smith, 1984). Tertiary-aged hipposiderids, which have been recovered from mainly karstic sediments in Europe, Africa and Australia, are referred to the genera *Palaeophyllophora*, *Asellia* and the subgenera *Hipposideros (Pseudorhinolophus)* Schlosser, 1887 (late Eocene-middle Miocene taxa), *Hipposideros (Brachipposideros)* Sigé, 1968 (late Oligocene-middle Miocene taxa) and *Hipposideros (Syndesmotis)* Peters, 1871 (middle Miocene-Recent taxa). *Hipposideros (Hipposideros)* has generally been reserved (e.g. by Sigé, 1968) for Recent hipposiderid species.

Riversleigh's *Brachipposideros nooraleebus* is known from thousands of specimens and dominates the vertebrate fauna of Microsite. All other vertebrate taxa in the deposit are known from at most a few specimens each. Microsite is the only Riversleigh fossil deposit dominated by a single bat species. Because of this, it has been possible to refer incomplete hipposiderid cranial material collected from Microsite to the single taxon *Brachipposideros nooraleebus*. Most of Riversleigh's other 150-plus Oligo-Miocene fossil vertebrate deposits contain between three and ten microchiropteran taxa (see Archer et al., 1991). French fossil faunas containing *Brachipposideros* species also commonly contain more than one hipposiderid taxon and no skull material referable to a species of *Brachipposideros* has previously been described.

In the present study, the skull of *H. (B.) nooraleebus* has been compared with the skulls of a modern representative of the genus *Hipposideros*, the type species *Hipposideros speoris speoris* of India and Sri Lanka; and a probable Recent descendant of the Australian *Brachipposideros* lineage, *Rhinonicteris aurantius* (Sigé et al., 1982).

Many striking differences distinguish *H. (B.) nooraleebus* from its congener *H. (H.) speoris*. In particular, differences were observed in: overall skull proportions; rostral morphology, including the size and position of the infraorbital and lacrimal foramina and maxillary fossa; morphology of the palate, premaxilla and zygomatic arch; attachment of the periotic to the surrounding basicranial elements; squamosal articulation with the paroccipital process; and, in the dentition, the reduced M3s, I^1 with reduced outer lobe, M^2 with less expanded heel, tall C_1 and small P_2. Similarities between the two skulls include the form of the sagittal crest and general shape of the braincase.

On the other hand, the skull of *H. (B.) nooraleebus* appears to be very similar in overall form to that of *R. aurantius*. Similarities include the general proportions of the skull, the broad rostrum,

subparallel tooth rows, morphology of the palate and zygomatic arch, the crested premaxillae, general basicranial morphology, very similar periotic and otic morphology, the pronounced accessory cusp on C^1 and little reduced upper and lower M3s. Obvious differences occur in the shape of the braincase and form of the sagittal crest.

In his study of the phyletic relationships of fossil hipposiderids, Legendre (1982) recognised that *Hipposideros* probably represents a paraphyletic group (see also Sigé, 1968) and that current taxonomy does not accurately reflect understanding about the evolutionary relationships of its supraspecific groups. Species of *Brachipposideros* have been recognised to have special affinities with small Recent species of *Hipposideros* (e.g. *H. caffer), Syndesmotis* and *Rhinonicteris* (Sigé, 1968; Legendre, 1982; Sigé et al., 1982). Those of *Pseudorhinolophus* appear to have affinities with species of *Asellia* and some large Recent *Hipposideros* species (e.g. *H. armiger, H. diadema* and *H. commersoni)* (Hugueney, 1965; Sigé, 1968; Legendre, 1982).

To refine understanding about the relationships of *Brachipposideros nooraleebus* to *Rhinonicteris aurantius* and other hipposiderids, further comparisons of skull and postcranial morphology of many additional hipposiderid groups are required. Pending this much larger study, comparisons made here support Sigé et al.'s (1982) hypothesis that the Australian taxa *B. nooraleebus* and *R. aurantius* are closely related.

ACKNOWLEDGEMENTS

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NIMBADON, A NEW GENUS AND THREE NEW SPECIES OF TERTIARY ZYGOMATURINES (MARSUPIALIA: DIPROTODONTIDAE) FROM NORTHERN AUSTRALIA, WITH A REASSESSMENT OF *NEOHELOS*

S. J. HAND, M. ARCHER, H. GODTHELP, T.H. RICH AND N.S. PLEDGE

Hand, S.J., Archer, M., Godthelp, H., Rich, T.H. & Pledge, N. S. 1993 06 30: *Nimbadon*, a new genus and three new species of Tertiary zygomaturines (Marsupialia: Diprotodontidae) from northern Australia, with a reassessment of *Neohelos*. *Memoirs of the Queensland Museum* 33(1): 193-210. Brisbane. ISSN 0079-8835.

Three new species of Oligo-Miocene zygomaturine diprotodontids are described from northern Australia. All are small, plesiomorphic and appear to comprise a distinctive clade of zygomaturines, named here *Nimbadon*. The clade is partly defined on the basis of the posteriorly inclined P^3 parastyle and blade extending from the parametacone to the lingual half of the P^3 crown and then to the anterolingual cingulum. Two of the species are known from Oligo-Miocene local faunas of Riversleigh Station, northwestern Queensland. The third is from the middle Miocene Bullock Creek Local Fauna of Camfield Station, northwestern Northern Territory. Description of additional fossil material referable to *Neohelos tirarensis* Stirton, 1967, a middle Miocene zygomaturine from the Kutjamarpu Local Fauna of South Australia, enables the genus to be distinguished from *Nimbadon*. The chronostratigraphic significance of the new zygomaturines is considered and found to approximately correspond to current understanding of the relative ages of the deposits from which the specimens were obtained. □ *Diprotodontidae, Zygomaturinae, Nimbadon, Neohelos, Oligo-Miocene, Riversleigh, Bullock Creek Local Fauna, Henk's Hollow Local Fauna, Fig Tree Local Fauna.*

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Specimens representing a very small zygomaturine were collected between 1984 and 1986 by Archer, Godthelp and Hand from the Henk's Hollow Site, in an as yet unnamed freshwater limestone on the Gag Plateau of Riversleigh Station (Archer, Hand & Godthelp, 1986; Archer & Flannery, 1987; Archer et al., 1989, 1991). Referred material includes maxillary and dentary fragments and isolated teeth. A second, larger Riversleigh species, represented by a maxilla, was collected in 1986 by Pledge from Fig Tree Site Locality adjacent to Godthelp Hill, Riversleigh Station.

A small Bullock Creek zygomaturine is known from a palate collected in 1981, by Rich and colleagues, from Horseshoe West Locality (WV 113) in the Camfield Beds of Camfield Station, northwestern Northern Territory (Rich et al., 1982, 1991).

Estimates of the age of the Henk's Hollow, Fig Tree and Bullock Creek Local Faunas are based mainly on stage-of-evolution comparisons of particular diprotodontian marsupials with those of other northern and central Australian faunas (Rich et al., 1982, 1991; Archer & Flannery, 1983; Archer & Hand, 1984; Woodburne et al., 1985; Murray, 1990a; Murray & Megirian, 1990; Archer et al., 1989,1991). Recent reappraisal of the age of central Australian Tertiary mammalian faunas, based on the study of foraminifera (Lindsay, 1987), suggests that some of these faunas (e.g. the Ditjimanka, Pinpa and Ericmas Local Faunas) are appreciably older than once thought (e.g. Woodburne et al., 1985; but see Tedford, 1966), possibly late Oligocene. By comparison, the Bullock Creek Local Fauna is estimated to be ?middle Miocene in age, i.e. immediately post-Wipajiri (Murray, 1990a; Murray & Megirian, 1990). On-going studies (Archer et al., 1991) of the Riversleigh fossil faunas suggest that the Henk's Hollow Local Fauna is ?middle Miocene in age and the Fig Tree Local Fauna somewhere between late Oligocene and early Miocene in age.

The new zygomaturines described here are most similar to forms currently referred to the genus *Neohelos*. Their generic distinction, however, has been clarified by discovery at the type locality of new material referable to *Neohelos*

TABLE 1. Measurements of *Neohelos tirarensis* P^3 (AMF87625) and M^3 (AMF87626) from the Leaf Locality, Lake Ngapakaldi, South Australia. In mm. Abbreviations: ant, anterior; post, posterior; paramet, parametacone; protoc, protocone; parac, paracone.

P^3	Length	15.8
	width	13.9
	width(paramet to protoc tips)	5.5
	height(paramet)	11.4
	height(parastyle)	6.5
M^3	length	18.8
	width(ant)	17.2
	width(post)	15.8
	height(parac)	7.8

tirarensis, the type and only named species of the genus. The original description (Stirton, 1967) of this Miocene zygomaturine from the Kutjamarpu Local Fauna of central Australia was based on five isolated teeth collected in 1962 at the Leaf Locality, Lake Ngapakaldi, Etadunna Station, South Australia. The holotype, a broken P^3, preserves only the posterior portion of the tooth. Though less complete than the other teeth, it was selected as the holotype because of the importance of premolar morphology in diprotodontoid systematics (Stirton, 1967; Stirton, Woodburne & Plane, 1967).

In 1982 two isolated teeth referable to *N. tirarensis* were collected from the type locality by Archer, Hand, T. Flannery, G. Hickie, J. Case and P. Bridge: a well-preserved RP^3 (AMF87625) and RM^3 (AMF87626). These add considerably to knowledge of this species. Additional materials referable to *Neohelos* from the Bullock Creek Local Fauna (Plane & Gatehouse, 1968; Plane, 1971; Murray & Megirian, 1992) and various Oligo-Miocene Riversleigh local faunas (Archer et al., 1989, 1991) are presently under study.

Institutional abbreviations used here are as follows: QMF, fossil collection of the Queensland Museum; AMF, fossil collection of the Australian Museum; SAMP, palaeontological collection of the South Australian Museum; NMVP, palaeontological collection of the Museum of Victoria; AR, research collection of the School of Biological Sciences, University of New South Wales. Cusp nomenclature follows Archer (1984) and Rich, Archer & Tedford (1978). The posterolingual cusp of the upper molars, conventionally called the hypocone (e.g. Stirton, Woodburne & Plane, 1967), is now called the metaconule following Tedford & Woodburne (1987) but the posterolingual cusp of P^3, following unchallenged convention, is called the hypocone. Cheektooth homology is that proposed by Archer (1978). Higher level systematic nomenclature follows Aplin & Archer (1987).

SYSTEMATICS

Superorder MARSUPIALIA Illiger, 1811
Order DIPROTODONTIA Owen, 1866
Family DIPROTODONTIDAE Gill, 1872
Subfamily ZYGOMATURINAE Stirton, Woodburne & Plane, 1967

Neohelos Stirton, 1967
(Fig. 1, Table 1)

Type species. Neohelos tirarensis Stirton, 1967

REVISED GENERIC DIAGNOSIS

The following combination of features appears to distinguish species of *Neohelos* from all other zygomaturines: P^3 with large, erect parastyle that is well isolated from the parametacone; parastyle is conical without tip developed as a blade; anterolingual basin well defined in P^3 by distinct basal cingulum extending between parastylar corner of tooth to anterolingual base of protocone; P^3 parametacone with an undivided tip; parametacone tip not developed into anterobucally oriented blade; line between protocone, parametacone and widest buccal point on crown is approximately rectilinear and divides crown either in half or leaves anterior division shorter than the posterior division; P^3 with well-developed hypocone or hypocone shelf; M^{2-3} with well developed parastyle and metastyle.

Nimbadon n.gen.
(Figs 2-5, Table 2)

Type species. Nimbadon lavarackorum n.sp.
Additional species. Nimbadon whitelawi n.sp., *Nimbadon scottorrorum* n.sp.

GENERIC DIAGNOSIS

Species of *Nimbadon* differ from those of all other zygomaturines (with special reference to *Neohelos*, the taxon to which they are otherwise most similar) in the following combination of features: small size (although they are larger than *Raemeotherium* Rich, Archer & Tedford, 1978); in having a molar gradient that does not appreciably increase posteriorly (in contrast to all other zygomaturines except *Raemeotherium*); posteriorly inclined parastyle on P^3 (rather than conical

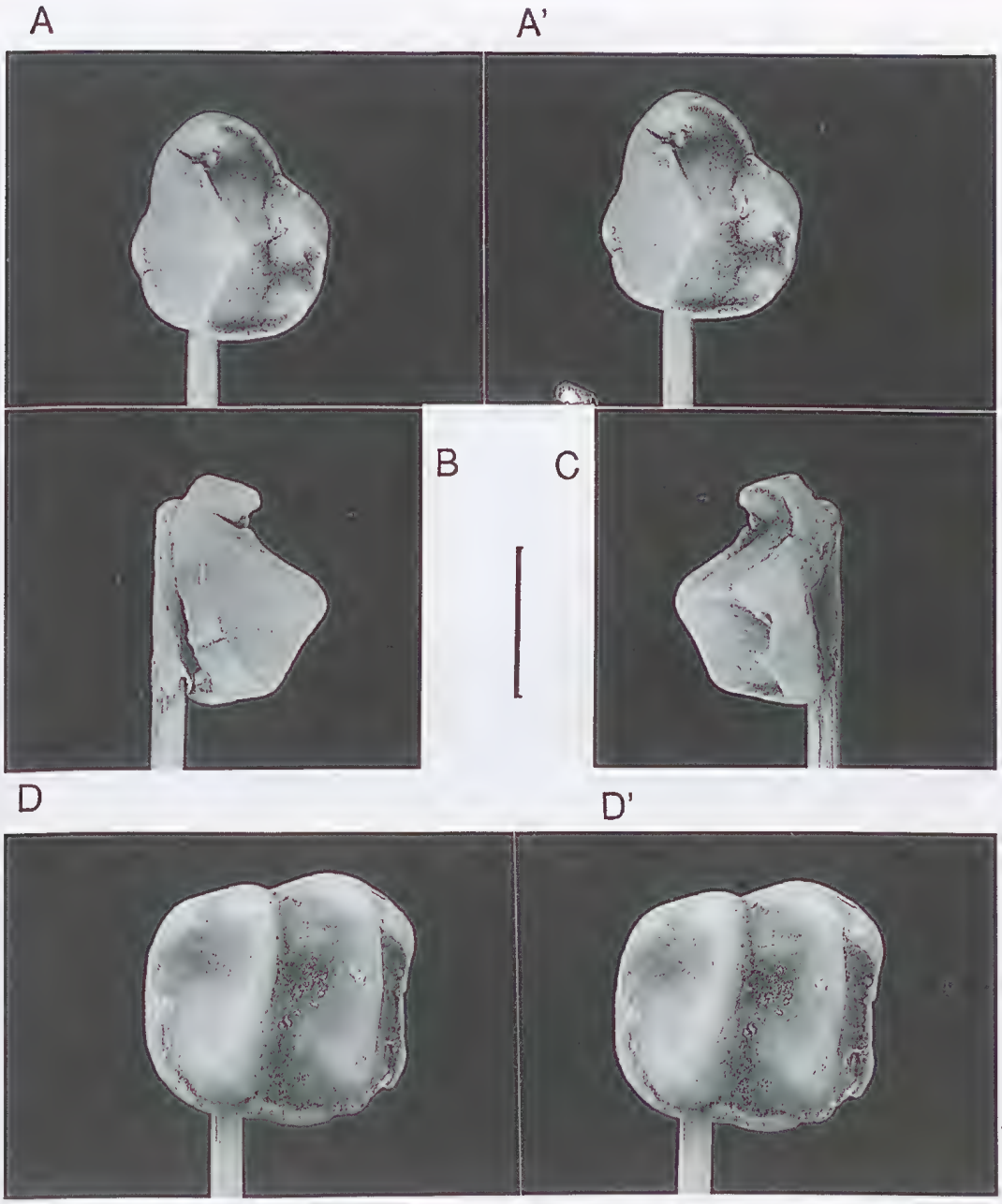

FIG. 1. *Neohelos tirarensis*, Leaf Locality, Lake Ngapakaldi, South Australia. AMF87625, RP^3: A-A', occlusal stereopair; B, buccal view; C, lingual view. AMF87626, RM^3: D-D', occlusal stereopair. Bar indicates 10mm.

and erect as in other zygomaturines except possibly *Plaisiodon centralis* Woodburne, 1967); an anterolingual blade on the parastyle of P^3 that surmounts a posterolingually oriented thegotic facette (in contrast to no apical blade such as may[?] characterise *Neohelos*); completely undivided parametacone on P^3 (in contrast to all other zygomaturines except *Neohelos* and *Alkwertatherium* Murray, 1990b); an anterobuccal blade on the parametacone of P^3 that surmounts an obliquely oriented anterolingual thegotic facette (in contrast to either no blade or a poorly developed anteriorly oriented blade such as may[?] characterise *Neohelos*); very small to absent hy-

TABLE 2. Measurements of *Nimbadon lavarackorum* n.sp., *N. whitelawi* n.sp. and *N. scottorrorum* n.sp. from Riversleigh and Camfield Stations, northern Australia. In mm. Brackets around figures indicate estimates. Abbreviations: ant, anterior; post, posterior; *Gag Site specimens.

LOWER DENTITION							
Species		*Nimbadon lavarackorum*					
QMF		23142	23153	23154	23155*	23158	23159
P_3	L	12.5	10.9				
	w	7.0	5.8				
M_2	L	14.0		13.3	13.0		
	w(ant)	8.4		8.5	8.3		
	w(post)	9.4		8.6	8.4		
M_3	L	15.4					
	w(ant)	10.1					
	w(post)	10.0					
M_4	L	15.5				14.0	
	w(ant)	11.0				10.6	
	w(post)	10.2				9.8	
M_5	L	15.9					14.3
	w(ant)	11.1					11.2
	w(post)	10.0					9.9
P_3-M_5	L	72.7					
M_{2-5}	L	60.9					

UPPER DENTITION														
Species		*Nimbadon lavarackorum*										N. whitelawi		*N. scottorrorum*
QMF		23141	23143	23144	23145	23146	23147	23148	23149	23150	23160*	NVM P186506		23157
												right	left	
P^3	L	12.7	14.1	12.4								12.9	13.0	14.3
	w			10.3								(10.4)	10.9	13.4
M^2	L	11.9			13.3						14.1	13.1	13.2	17.1
	w(ant)	10.2			10.9						11.3	(9.3)		15.0
	w(post)	9.9			10.8						10.5	9.2		15.8
M^3	L	12.3				13.7					14.3	13.1		17.9
	w(ant)	11.3									11.6	10.9		
	w(post)	10.1				10.9					10.4	(9.5)		
M^4	L						13.8		14.3			13.5		18.5
	w(ant)						11.5		12.2			11.1		
	w(post)						10.7	12.5	10.4			9.7		
M^5	L									13.5				18.1
	w(ant)									11.3				
	w(post)									9.8				
Palate width												29.2		
P^3-M^5	L													(84.4)
P^3-M^4	L											52.8		66.3
P^3-M^2	L											25.3	25.8	48.2
M^{2-5}	L													(71.5)
M^{2-4}	L											39.5		53.1

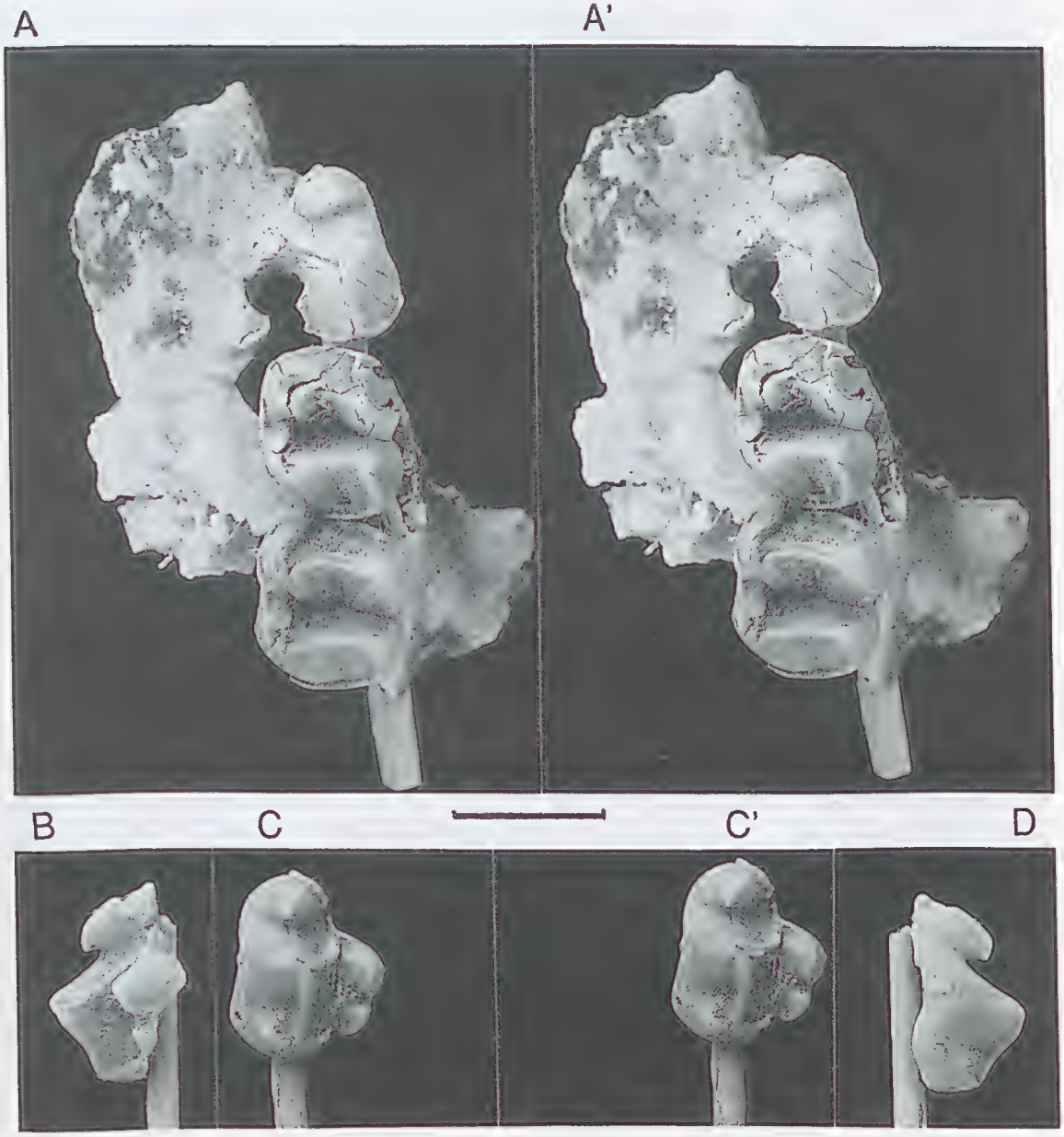

FIG. 2. *Nimbadon lavarackorum* n.gen., n.sp., Henk's Hollow Site, Riversleigh Station. A-A', QMF23141, holotype, left maxillary fragment with M^2, M^3 and buccal half of P^3, occlusal stereopair. B-D, QMF23143, RP^3: B, lingual view; C-C', occlusal stereopair; D, buccal view. Bar indicates 10mm.

pocone on P^3 (in contrast to *Alkwertatherium* and most but not all *Neohelos* and in contrast to all other zygomaturine P^3s where this cusp is large, including *Maokopia* Flannery, 1992); posterobuccal basal cingulum on P^3 (in contrast to most other zygomaturines except *Alkwertatherium* and *Neohelos* where this feature is variably developed); poorly developed to absent anterolingual basal cingulum joining base of parastyle to base of protocone (in contrast to most other zygomaturines except some *Neohelos* where there may be only a very small cingulum); an anterolingual crest on P^3 that extends from the parametacone towards the protocone but, veering

anteriorly, bypasses the buccal crest from the protocone and extends to the anterolingual basal cingulum (in contrast to directly connecting to the buccal crest from the protocone as occurs in most if not all other zygomaturines); a line extended buccally through the protocone and parametacone passes anterior to the position of the widest point on the buccal base of the crown (in contrast to intersecting this point as it does in *Neohelos* and *Alkwertatherium*, although this feature is variable in *Nimbadon whitelawi* n.sp.); this same line divides the crown such that the anterior moiety is longer than the posterior one (as it does in *Alkwertatherium* but in contrast to either dividing the crown into approximately equal lengths or into shorter anterior and longer posterior moieties as it does in *Neohelos*); poorly developed parastyles and metastyles on upper molars (in contrast to species of *Neohelos* but as in some anterior teeth of other zygomaturines such as *P. centralis*).

ETYMOLOGY

Nimba is a northwestern Queensland Aboriginal word (Wanyi language) meaning 'small'; *don* is Greek for 'tooth'. The name alludes to the small molars found in species of this genus and to the fact that the posterior molars do not increase markedly in size from M2 to M4 as they appear to do in the otherwise similar *Neohelos tirarensis*.

Nimbadon lavarackorum n.sp.
(Figs 2,3)

HOLOTYPE

The holotype is QMF23141, a left maxillary fragment containing M^2, M^3 and the buccal half of P^3.

ETYMOLOGY

The species is named after Sue and Jim Lavarack in recognition of their invaluable support in the field at Riversleigh and as founding members and hard working Councillors of the Riversleigh Society, a support group for Australian palaeontological research.

TYPE LOCALITY AND AGE

Henk's Hollow Locality (Archer & Flannery, 1987) occurs within the sequence of Tertiary limestones outcropping on Riversleigh Station, northwestern Queensland (Archer & Hand, 1984; Archer et al., 1989, 1991). It is stratigraphically near the top of the System C sequence as defined by Archer et al. (1989, 1991). This is interpreted to be stratigraphically higher than Site D (System A containing the Riversleigh Local Fauna; Archer et al., 1991), Microsite (containing the Nooraleeba Local Fauna; Sigé, Hand & Archer, 1982; Hand, 1993) and Gag Site (near the base of System C, containing the Dwornamor Local Fauna; Flannery & Archer, 1984; Hand, 1985; Archer et al. 1991), but is close to (though still above) the level of Two Trees Site (containing the Two Trees Local Fauna Flannery & Archer, 1987). On the basis of its stratigraphic position and stage of evolution comparisons of its fossil mammals (work in preparation), the Henk's Hollow Local Fauna is tentatively interpreted here to be middle Miocene in age (Archer et al., 1989, 1991).

REFERRED SPECIMENS AND THEIR LOCALITIES

QMF23142 from the Henk's Hollow Locality, a left dentary containing P_3-M_5, is tentatively referred to this species, as are the following isolated teeth from Henk's Hollow: QMF23143, a right P^3; QMF23144, a left P^3; QMF23145, a left M^2; QMF23146, a right M^3; QMF23147, a left M^4; QMF23148, a left ?M^4; QMF23149, a right M^4; QMF23150, a right M^5; QMF23151, a right P_3; QMF23152, a left P_3; QMF23153, a right P_3; QMF23154, a left ?M_2. QMF23155, a right M_2, and QMF23160, a right M^{2-3}, were collected from the Gag Site of the same plateau, Riversleigh Station.

REFERRED LOCALITIES AND AGES

The stratigraphic relationships of the Henk's Hollow Local Fauna and the Dwornamor Local Fauna are indicated above. At present, both are interpreted to be middle Miocene in age.

SPECIES DIAGNOSIS

This species is distinguished from *Nimbadon scottorrorum* n.sp. from Riversleigh's Fig Tree locality (see below) by its smaller size, relatively longer P^3, better developed hypocone on P^3, less well-developed parastyle on M^3 and probably more elongate posterior upper molars and less well developed postmetacrista but more discrete metastyle on M^2.

It is distinguished from the similar-sized *N. whitelawi* n.sp. by its almost square (rather than rectangular) upper molars.

DESCRIPTION

P^3 is represented by three specimens: a LP^3 from the holotype, QMF23141; an isolated RP^3, QMF23143; and an isolated LP^3, QMF23144. The tooth is widest across the protocone, sharply pinching in anteriorly and smoothly rounding posteriorly. It is subtriangular and is comprised

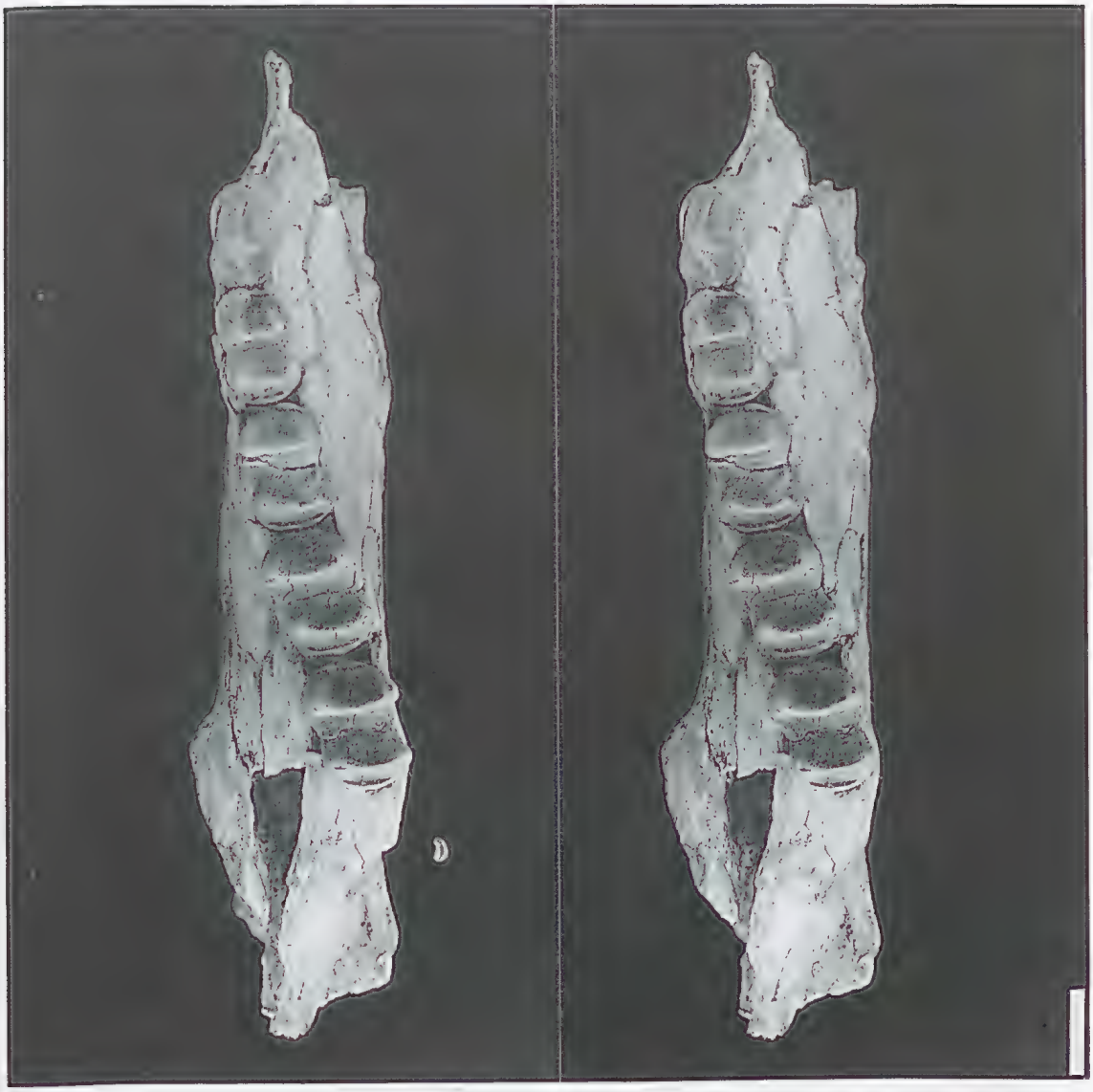

FIG. 3. *Nimbadon lavarackorum* n.gen., n.sp., Henk's Hollow Site, Riversleigh Station. QMF23142, left dentary with P_3, M_2, M_3, M_4 and M_5, occlusal stereopair. Bar indicates 10mm.

of four cusps: the parastyle, parametacone, protocone and hypocone (the latter however being variably developed). The parametacone is the highest cusp. It is blade-like with a strong shearing crest on the posterior edge and a short anterobucally oriented apical crest. The protocone and parastyle are subequal to each other in size. The hypocone is the smallest cusp and is even absent in one specimen (QMF23144). There is no suggestion of a division in the parametacone which is pyramid-shaped having relatively flattened anterior, buccal and lingual faces. The protocone is lingual to the parametacone and the hypocone lies posterobuccal to the protocone. The hypocone is more sharply separated by deep fissures from the buccal cusps than is the protocone. The parastyle is posteriorly inclined with a short anterolingually oriented apical blade. This large conical cusp forms a strong anterobuccal projection in the occlusal outline of the crown. It is separated from adjacent cusps by a chevron-shaped transverse cleft that is better-developed lingually than buccally. Posterior to this cleft, and on the anterior flank of the parametacone, a con-

spicuous ridge extends anterolingually from the tip of the parametacone to the anterolingual cingulum at a point anterobuccal to the base of the protocone. From the tip of the protocone, a poorly-defined transverse crest runs buccally until it almost meets (but does not) the parametacone ridge, its counterpart, at the commisure that separates the protocone and parametacone. Anterolingually, a very poorly developed (to ?absent) cingulum extends from the anterobuccal base of the protocone to the lingual base of the parastyle but does not continue up the flank of the parastyle. A cingulum is also developed posterobuccally from the buccal flank of the parametacone to the most posterior point of the crown (but is better-developed in some specimens than in others) and appears to be developed posterolingually from this point to at least the base of the hypocone. There is no evidence of an anterobuccal cingulum. From the tip of the parametacone, a prominent crest runs to the posterior margin of the tooth, dividing the posterolingual and posterobuccal cingula. A small crest runs posteriorly from the tip of the protocone to a swelling or cuspule. Another thin crest on the posterior face of the hypocone appears to converge with the posterolingual cingulum (at least in QMF23144). The tooth is two-rooted. The anterior root is conical and slightly anteriorly sloping; the larger posterior root is anteroposteriorly flattened and anteriorly convex. Many of the medial surfaces of the four crowns are covered in fine, poorly developed crenulations. There are two roots: one anterior oval one beneath the parastyle; and a much longer anteroposteriorly compressed root that extends transversely beneath the whole width of the posterior part of the crown.

M^2. The first upper adult molar is known from the holotype, QMF23141, and ?an isolated left M^2, QMF23145. It is a low-crowned almost square transversely lophodont tooth that is only slightly longer than wide. It is comprised of an anterior moiety, the protoloph, and a posterior moiety, the metaloph. Both are anteriorly convex. The paracone and metacone are similar in size as are the slightly shorter protocone and metaconule. The metaconule is slightly higher than the protocone and more lingually-situated. The metaloph is thus wider than the protoloph. The paracone and metacone are slightly closer together than are the protocone and metaconule. In the anterobuccal corner of the tooth a weak parastyle is developed at the buccal end of the short anterior cingulum. There is no metastyle although there is a prominent postmetacrista that extends from the tip of the metacone to the posterior cingulum with which it merges. A weakly developed postparacrista on the posterior flank of the paracone extends toward the midvalley but stops short of contacting similar premetacristae that extend from the metacone and from just lingual to the metacone towards the midvalley. From the protocone and metaconule, wide but very faint crests extend posterobuccally across the posterior flanks of the protoloph and metaloph. From the protocone, this crest extends to the transverse valley near the midline; from the metaconule this crest extends to the posterior cingulum also near the midline of the tooth.

Wear facettes on these crests exhibit polish and parallel striations (particularly in QMF23145) suggesting that their function was maintained by thegosis against (respectively) the entoconid of M_2 and the metaconid of M_3. The anterior cingulum extends from the parastyle around the lingual base of the protocone where it is interrupted and then continues across the lingual end of the transverse valley to the anterolingual base of the metaconule where it is interrupted and then continues around to the metastyle. There is no buccal cingulum. The M^2 may have been three-rooted with a cylindrical root beneath the paracone and another beneath the protocone and a single wide root beneath the metaloph. Precise thegotic facettes occur on the anterior trailing edges of the protoloph and metaloph blades. The anterior flanks of the protoloph and metaloph are "hollow-ground" in anticipation of the thegotic sharpening of the blades. Fine vertical crenulations on the flanks of the protoloph and metaloph produce secondary, vertical ?beta thegotic blades as the tooth sustains abrasive and thegotic wear.

M^{3-5}. M^{3-5} are similar to M^2 in basic morphology but are slightly larger and higher-crowned. The paracone is larger and more buccally- situated than the metacone. The protoloph and metaloph increase slightly in width from M^{2-4}. The parastyle and postmetacrista are markedly reduced in M^{3-5} such that in M^3 they are represented by terminal swellings in the anterior and posterior cingula respectively and are absent in M^4 and M^5. In some specimens (e.g. M^3 in QMF23160), however, there is a very tiny cuspule on the posterior flank of the metacone of posterior molars. The postparacrista is less well-developed as are the crests from the protocone and metaconule. The mesostyle appears to be lacking. The part of the crown anterior to the protoloph is shorter and the swelling in the transverse valley better developed. The metaloph is much more strongly curved in

M^{3-5} and is more lingually offset with respect to the protoloph.

Dentary. QMF23142, a dentary containing P_3, M_{2-5}, is tentatively referred to this species. It is of a size appropriate for some of the referred upper molars of this species and in its suite of plesiomorphic zygomaturine features (e.g. its lack of a posteriorly increasing molar size gradient), is analogous to the phylogenetic state of the upper molars of *N. lavarackorum*. However, because the specimen appears to be approximately 10% larger than the holotype, there is still some slight doubt about the propriety of referring this dentary to *N. lavarackorum*.

The dentary is badly fractured and is missing the incisor, medial symphysis, angle and ascending ramus. It is deepest below the hypolophid of M_4. The ventral border slopes posteriorly upward from this point and anteriorly upward to at least the hypolophid of M_2. The anterior edge of the coronoid process leads posterodorsally from the body of the horizontal ramus. The postalveolar process is missing. There is no distinct digastric fossa and the area beneath the leading edge of the coronoid process is smooth suggesting that the masseteric fossa was not deep. The mental foramen is located approximately 4mm in front of a vertical line marking the most anterior edge of the P^3 crown. It is round in lateral view and opens anterodorsally onto the buccal surface of the diastemal region. Although the mandibular foramen is not preserved, the mandibular canal is represented by a sulcus at about the level of the tooth row.

The P_3 is preserved in QMF23142 as well as QMF23152, an isolated LP_3, QMF23153, an isolated RP_3 and QMF23151, an isolated RP_3. The tooth is longer than it is wide and more narrow anteriorly than posteriorly. It bears a central principal cusp, the protoconid, and a much smaller medially positioned posterior cingular cusp. These are joined by a prominent longitudinal shearing crest that also extends anteriorly from the protoconid to terminate as a cuspule or cingular swelling at the anterior edge of the crown. Lingual to the principle central cusp there is a variably distinguished cuspule (stylid or vertical cristid). This structure is the apex of a vertical flanking crest that extends ventrally to a point just posterior to the lingual base of the protoconid. This crest is most conspicuous in posterior view. A posterolingual cingulum leads posteriorly from the base of this crest to the base of the posterior cusp. A similar but much less well-developed vertical cristid extends ventrally from the buccal apex of the protoconid. Taken together, these flanking cuspules and their associated vertical cristids comprise a transverse structure that intersects the crown at its apex at right angles to the main longitudinal shearing cristid. The posterior cingulum is much better developed than the anterior cingulum which is present only at the anterolingual tip of the crown. The posterior cingulum extends from the lingual base of the protoconid to the posterior cuspid where it is met by the buccal base of the protoconid but is best developed in the region of the posterior cuspid where it is met by the main longitudinal crest of the crown. In this area of intersection, the posterior cingulum is conspicuously crenulated in some specimens (i.e. QMF23152 and QMF23153) and slightly less so in others (i.e. QMF23151). In QMF23152, a wear facette on the posterobuccal cingulum, possibly produced by the P^3 parametacone, is developed which is not seen in other specimens. In this same specimen, just anterior to the crenulated posterior cingulum, a transverse crest extends anterolingually from the tip of the posterior cusp to the posterolingual cingulum. In all specimens, a wear facette for M_2 is developed at the tallest point of the posterior cingulum. The tooth is double-rooted, the anterior root being conical in shape, the posterior root being anteroposteriorly flattened.

Specimens QMF23152 and QMF23153, although similar in morphology, are considerably smaller than the P_3 preserved in the dentary. The P_3 in this species might be sexually dimorphic.

M_2. The M_2, known from QMF23142 and QMF23154? (and the Gag Site QMF23155), is an elongate, subrectangular tooth that is narrower anteriorly than posteriorly. The trigonid of M_2 is represented by a transverse protolophid and an arcuate anterolingually directed paracristid that extends to the anterior margin of the tooth. From the protoconid a short indistinct crest (?protocristid) appears to extend posterobuccally to terminate in a slight swelling which is perhaps the protostylid. From the metaconid, a crest extends anteriorly a short distance. From the entoconid, a short entocristid extends anterolingually.

In occlusal view, the paracristid is convex buccally, the protolophid is transverse or very slightly posteriorly convex and the hypolophid is markedly posteriorly convex. The protolophid is narrower than the hypolophid. An anterior cingulum is present both buccal and lingual to the anterior end of the paracristid. The cingulum on the buccal side is not preserved in QMF23142, is distinct (between the protolophid and hypolo-

phid) in QMF23155 but not in QMF23154. There is no lingual cingulum or cristid obliqua in QMF23142 but there is a lingual cingulum in QMF23155 (again between the protolophid and hypolophid). The posterior cingulum connects the posterior base of the hypoconid to that of the entoconid. A wear facette is developed at the midpoint of the posterior cingulum. Distinct wear facettes extend along the posterior lengths of the protolophid and hypolophid. In lingual view, the floor of the transverse valley is U-shaped. The protoconid is taller than the subequal metaconid, hypoconid and entoconid. The tooth is double-rooted but these are not well preserved in the isolated teeth QMF23154 and QMF23155.

QMF23154 (M_2?) has a paracristid and premetacristid that are much less distinct than those preserved in the dentary and Gag Site specimen. Only the paracristid extends to the anterior cingulum of the tooth. In this specimen, the enamel on the posterior face of the protolophid has prominent vertical crenulations. The cristid obliqua is also distinct although low and extends as a minor vertical crenulation on to the posterior flank of the protolophid.

M_{3-5}. Unlike M_2, trigonids of the posterior molars lack a prominent paracristid and are more rectangular in appearance with the protolophid being slightly wider than the hypolophid in M_{3-5}.

In M_3, the protolophid and hypolophid are approximately the same width. The paracristid forms a poorly-defined vertical crest that extends only partly down the anterior face of the protolophid. The premetacristid is also poorly defined and extends approximately the same distance. Protolophids and hypolophids become more posteriorly convex from M_2 to M_5. In M_{4-5}, the protolophids are markedly wider and the hypolophids are lingually displaced. M_4 and M_5 are larger than M_3.

Nimbadon whitelawi n.sp.
(Fig. 4)

Holotype
The holotype and only known specimen is NMVP186506. It preserves the palate, RP^3-M^5 and LP^3-M^3. All teeth except LP^3 are damaged and LM^3 and RM^5 are missing parts of their posterior halves.

Etymology
This species is named after Michael Whitelaw who assisted in the collection and processing of specimens from Bullock Creek.

Type Locality and Age
The type locality is fossil vertebrate locality WV 113 in Bultitude (1973) (17°7'S, 131°32'E), the Horseshoe West locality of the Camfield Beds at Bullock Creek, Camfield Station, northwestern Northern Territory. The Bullock Creek Local Fauna (Plane & Gatehouse, 1968; Archer & Bartholomai, 1978; Rich et al., 1991; Archer & Hand, 1984; Murray & Megirian, 1990, 1992) is currently interpreted to be ?middle Miocene, i.e. immediately post-Wipajiri, in age (Woodburne et al., 1985; Murray, 1990a; Murray & Megirian, 1990, 1992).

Species Diagnosis
This species is distinguished from *N. lavarackorum* and *N. scottorrorum* by its markedly more elongate (i.e. less square) upper molars and relatively more anteriorly situated buccal swelling on P^3. It is also distinguished from *N. scottorrorum* by its relatively much longer P^3 and markedly convex anterior and posterior molar crown margins such that these teeth have a much reduced area of interdental contact.

Description
The species is described insofar as it differs from *Nimbadon lavarackorum*.

The palate preserves most of the right and a large part of the left maxillae and small fragments of the left and right palatines. Anteroventrally, the palate is fractured at or behind the premaxillo-maxillary suture. Posteroventrally, it preserves the maxillo-palatine suture. The latter extends anteriorly to a point medial to the posterior part of M^3. Palatal ridges extend longitudinally and anteriorly along the length of the palate from the level of M^3. The right diastemal crest runs anterolingually. The tooth rows are parallel to slightly convex buccally. Anteriorly, doming of the median region of the palate is marked. It extends posteriorly to the level of the rear of M^2 and, though shallowing perhaps, anteriorly to at least just behind the premaxillo-maxillary boundary. There is a pair of nutrient foramina on the right side of the palate medial to P^3 and on the left side a single foramen. Medial to the hypoloph of M^2, is another tiny foramen on each side of the palate. The infraorbital foramen canal is about 30mm in length. The infraorbital canal opens onto the face 14mm above the anterior edge of the P^3 alveolus. Sutural relationships of the palatine, lacrimal, jugal and maxillary bones are unclear. There is no evidence for maxillary or palatal vacuities although the anterior and posterior ex-

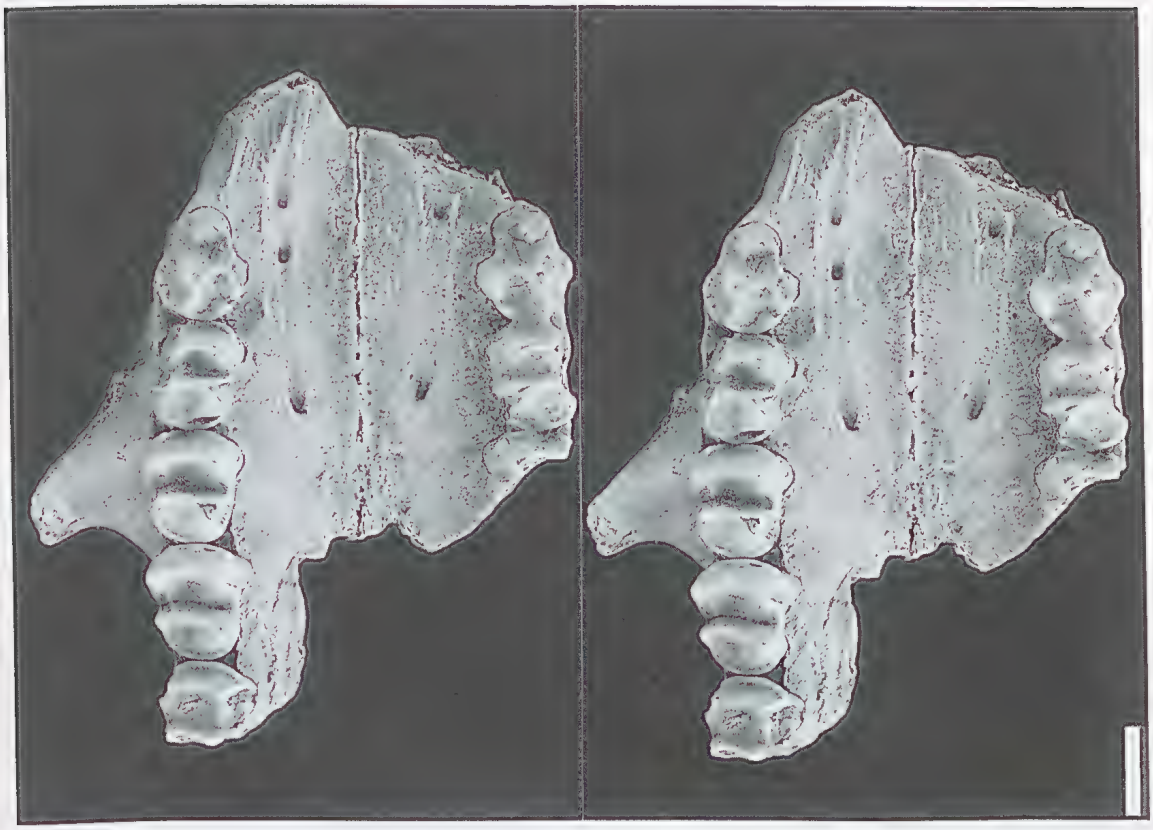

FIG. 4. *Nimbadon whitelawi* n.sp., Bullock Creek, Northern Territory. NMVP186506, palate with RP^3-M^5 and LP^3-M^5, occlusal stereopair. Bar indicates 10mm.

tremities of the palate are missing. The maxillary process near the roof of the zygomatic arch, although damaged, is down-turned and conspicuous but does not extend ventrally below the level of the palate. There appears to have been a very reduced orbital wing of the maxilla, although bone boundaries in this region are unclear.

Upper dentition. The P^3 differs from most specimens (all except QMF23144 AR5513) of *N. lavarackorum* in the greater degree of development of the hypocone. In *N. whitelawi* the parastyle appears to be less posteriorly inclined and the anterolingually-directed crest that extends from the parametacone to the anterolingual cingulum is less distinct although it is possibly diminished by wear. It nevertheless approaches the buccal crest from the protocone at a steep angle rather than perpendicular.

The M^2 on both sides of the holotype is damaged buccally and lingually. However, it appears to differ from both Riversleigh species of *Nimbadon* in being longer relative to P^3 and in appearing to be rectangular rather than square.

The M^3 appears to differ from the Riversleigh species in a similar way as M^2, but it appears to be relatively even more elongate. M^2 and M^3 are approximately equal in length.

The M^4 differs less from that tooth in the other species of *Nimbadon*.

All of the cheekteeth of *N. whitelawi* appear to differ from those of *N. scottorrorum* in having anteriorly and posteriorly markedly convex tooth margins so that the crowns abut with limited contact.

Nimbadon scottorrorum n.sp.
(Fig. 5)

HOLOTYPE

The holotype and only known specimen is QMF23157 (formerly SAMP27815), a right maxillary fragment containing P^3, M^2, M^3, M^4 and M^5. While P^3 and M^2

are intact, M^{3-5} are missing the buccal margins of the crown.

Etymology

The species is named after Sue and Don Scott-Orr, in recognition of their long-term support for the Riversleigh Palaeontological Research Project. With the Lavaracks, they are also founding members and Councillors of the Riversleigh Society.

Type Locality and Age

The type locality, Fig Tree Site, is adjacent to Godthelp Hill, Riversleigh Station, northwestern Queensland. It is laterally adjacent to units regarded by Archer et al. (1989, 1991) to be part of System B although it may actually be from the basal part of System B or even upper part of System A, hence stratigraphically below Henk's Hollow (upper part of System C; Archer, Hand & Godthelp, 1986) and Gag Site (lower part of System C; Flannery & Archer, 1984; Hand, 1985) and possibly above or equivalent to Microsite (?System A; Sigé, Hand & Archer, 1982; Archer et al., 1989, 1991) and Site D (System A; Tedford, 1967; Archer et al., 1989, 1991). On this basis and stage of evolution comparisons of the marsupials in these faunas, the Fig Tree Local Fauna is interpreted to be ?late Oligocene-early Miocene in age.

Species Diagnosis

This species is distinguished from *Nimbadon lavarackorum* and *N. whitelawi* by its larger size, anteroposteriorly compressed P^3 (which is much shorter than any upper molar), its more robust cingula on all cheekteeth and its greater parastylar development in M^{2-3} (contributing to the squared appearance of these teeth). It also has less convex anterior and posterior molar crown margins which therefore have much wider interdental contact with each other.

It is further distinguished from most (but not all) *N. lavarackorum* by its much smaller hypocone on P^3.

Description

Nimbadon scottorrorum differs from *N. lavarackorum* and *N. whitelawi* as follows:

The P^3 is markedly anteroposteriorly compressed such that it is almost as wide as it is long and is subrounded in shape. Unlike *N. lavarackorum*, in which P^3 is equal in length or longer than any adult upper molar, in *N. scottorrorum* this tooth is the shortest in the tooth row. The hypocone appears to have been very poorly developed.

The anterobuccal corner of M^2 has a much squarer appearance due to greater parastylar development in the anterior cingulum. This is true also of the posterobuccal corner of the tooth where metastylar development occurs mid-way along the postmetacrista.

Parastylar development in M^3 is relatively marked compared with its condition in *N. lavarackorum*. The teeth are buccally fractured in M^{3-5} making it impossible to determine the degree of development of the buccal cusps in M^{4-5}.

DISCUSSION

The three diprotodontids described here appear to comprise a new clade of zygomaturines. As species of the new genus *Nimbadon*[1], they may be distinguished from other zygomaturines by, among other features, a combination of upper premolar attributes. Premolar morphology was extensively used by Stirton (1967) and Stirton et al. (1967) to help resolve distinctions between diprotodontid lineages and has subsequently been used by most workers. Few other character systems have been found to be as useful in distinguishing probable inter-relationships among Tertiary diprotodontids.

Since Stirton et al.'s (1967) review of Tertiary diprotodontids, diverse diprotodontoid materials have been collected from Oligo-Miocene fossil sites at Riversleigh, Bullock Creek, Alcoota and Beaumaris and from Pleistocene sites in New Guinea (e.g. Flannery, 1992) and many areas of Australia. This material includes specimens representing new genera and probably new diprotodontoid subfamilies. Murray (1986, 1990a,b) has named several new Tertiary taxa but the bulk of the material, particularly from Riversleigh sites, is yet to be described. As a result of the new discoveries, the superfamily Diprotodontoidea is in need of major revision.

At present (e.g. the reviews of Archer, 1984; Aplin & Archer, 1987; Marshall, Case & Woodburne, 1989; Murray, 1990b) two diprotodontoid families are recognised: the Palorchestidae; and the Diprotodontidae with two subfamilies, the

[1] The generic name *Nimbadon* was used by Murray (1990b) in a cladogram of hypothetical phylogenetic inter-relationships among Miocene diprotodontids. However Murray did not designate a species of *Nimbadon* in the cladogram or in the ensuing discussion, and, as outlined in Article 13B of the Code of Zoological Nomeneclature, '*Nimbadon*' was thus used as a *nomen nudum*.

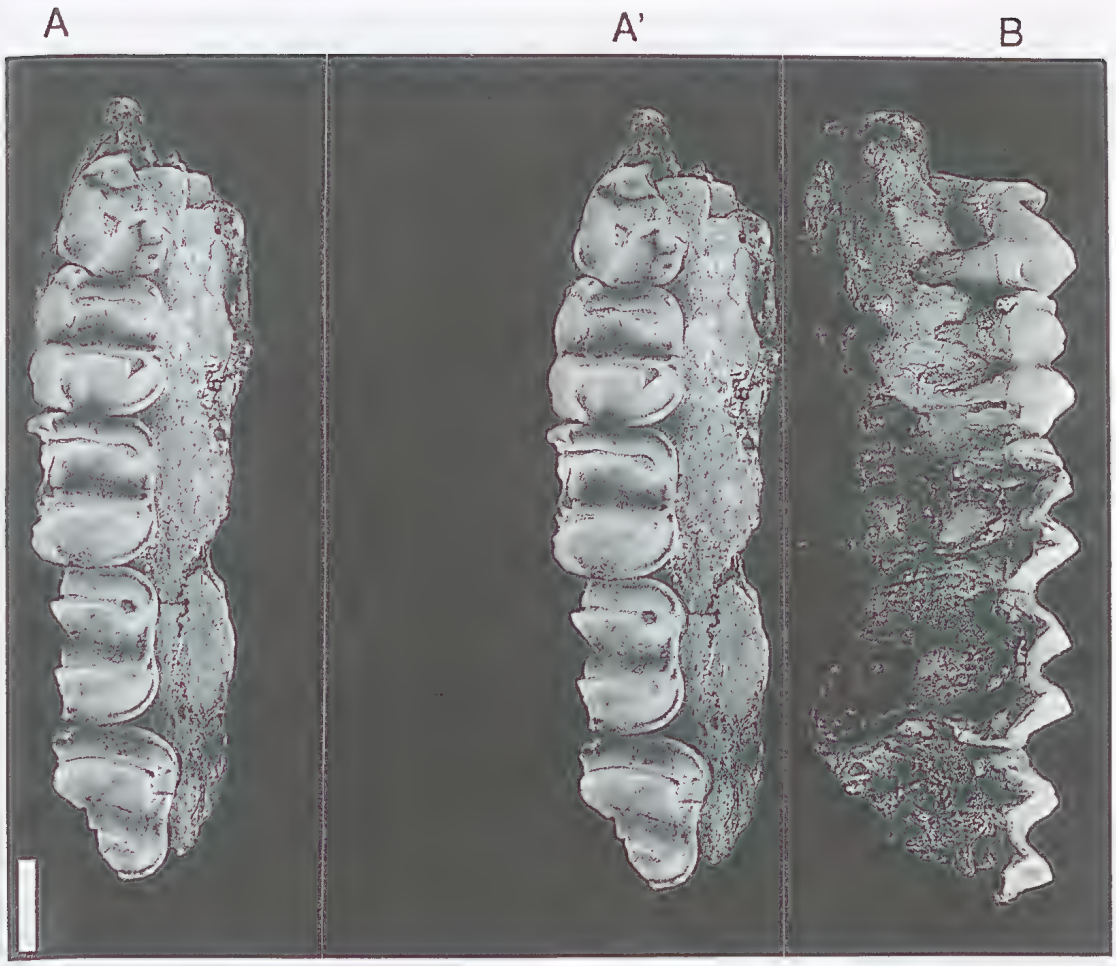

FIG. 5. *Nimbadon scottorrorum* n.sp., Fig Tree Site, Riversleigh Station. QMF23157, right maxillary fragment with RP^3- M^3, A-A', occlusal stereopair; B, buccal view. Bar indicates 10mm.

Diprotodontinae and the Zygomaturinae. Although zygomaturines have traditionally (e.g. Stirton et al., 1967) been considered to be among the most primitive of diprotodontoids, it is by no means certain that this is so (Murray, 1990b). It is not clear what might be used as an appropriate outgroup in a phylogenetic analysis of zygomaturines nor, consequently, are polarities of character state morphoclines within the Zygomaturinae confidently determined.

Murray (1990b) has discussed other difficulties in analysing diprotodontid phylogenetics. He notes that despite the fact that many Tertiary diprotodontids are represented by almost-complete skull and dentary material, discontinuities in some character complexes and the continuously varying nature of others tend to obfuscate clarification of relationships between taxa. Considerable variability in cranial morphology has been observed in some zygomaturines (e.g. in a *Neohelos* sample from the Bullock Creek Local Fauna; P. Murray, pers.comm.), and the molar dentitions of the zygomaturines *Plaisiodon centralis* Woodburne, 1967 and *Alkwertatherium webbi* Murray, 1990b and the diprotodontine *Pyramios alcootense* Woodburne, 1967 have been found to overlap in size and morphology (Murray, 1990b).

It is perhaps a measure of the difficulties encountered in determining species and generic boundaries for diprotodontids that *Nimbadon* is one of few non-monotypic Tertiary zygomaturine genera, the others being *Kolopsis* Woodburne, 1967 and *Zygomaturus* Owen, 1859.

Recognition of the genus *Nimbadon* has been facilitated by re-diagnosis of *Neohelos* Stirton,

1967 based on new material obtained by Archer and colleagues 20 years after the original material was collected by Stirton and colleagues from the Leaf Locality of Lake Ngapakaldi, South Australia. This provides novel information about the anterior morphology of P^3, which exhibits, among other distinctive features, a large, erect parastyle. This feature is also present in specimens referred to *Neohelos* from the Bullock Creek and Riversleigh Tertiary faunal assemblages (Plane & Gatehouse, 1968; Plane, 1971; Rich et al., 1982; Murray & Megirian, 1990, 1992; Archer et al., 1989, 1991).

In his review of Oligo-Miocene diprotodontid taxa, Murray (1990b) postulates a number of phylogenetic hypotheses, only one of which is expressed in his cladogram (fig. 14). The latter is based primarily on analysis of dental characters (in particular, P^3), using species of the Oligo-Miocene palorchestid genera *Ngapakaldia* and *Pitikantia* as outgroups. In it, Murray identifies species of *Kolopsis* and *Zygomaturus* as the most derived diprotodontids and *Neohelos tirarensis* as their closest relative. Species of *Nimbadon* form the sister-group to the *Neohelos–Kolopsis–Zygomaturus* clade, with *Plaisiodon centralis* being the sister-group of a *Nimbadon–Neohelos–Kolopsis–Zygomaturus* clade, *Kolopsoides cultridens* Plane, 1967 the sister-group of a *Plaisiodon—Nimbadon—Neohelos—Kolopsis—Zygomaturus* clade and *Alwertatherium webbi* the most plesiomorphic of zygomaturines. Species of *Pyramios*, *Euryzygoma*, *Bematherium* and *Diprotodon* form a separate (diprotodontine) clade. *Raemeotherium yatkolai* Rich, Archer & Tedford, 1978 from the ?late Oligocene Namba Formation of Lake Pinpa, South Australia, is interpreted to be the most plesiomorphic member of the family Diprotodontidae.

On the basis of his broader study of dental and cranial characters, however, Murray (ibid.) concludes that there are probably two minor zygomaturine lineages: one represented by species of *Nimbadon*, *Neohelos* and *Kolopsis*, a group he suspects may consist of taxa related largely by symplesiomorphies; the other lineage possibly containing species of *Alkwertatherium*, *Plaisiodon* and *Kolopsoides*, although for this clade he can find even less concrete evidence. He suggests that these two lineages might be related through common ancestry in *Nimbadon*. He also suggests in the text, but not the cladogram, that *Nimbadon* species could represent basal zygomaturines with some specific affinity to *Plaisiodon centralis* and *Neohelos tirarensis*, and that *Plaisiodon centralis* is more closely related to *Alkwertatherium webbi* than to any other zygomaturine.

A phylogenetic hypothesis of diprotodontid inter-relationships, including the three new *Nimbadon* species and broadly based on Murray's cladistic analysis of dental characters, is given in Fig. 6. The polarity of some characters has been interpreted differently from Murray (1990b) but basic intergeneric relationships remain unchanged except for the position of *Plaisiodon centralis*.

In Fig. 6 and Murray (1990b), the Zygomaturinae are clustered on the basis of a large parastyle on P^3 which is separated from the parametacone by a deep cleft. The *Kolopsoides-Plaisiodon-Nimbadon-Neohelos-Kolopsis-Zygomaturus* clade shares as a synapomorphy development of a hypocone in P^3. The basic proportions of P^3 are apomorphically shared by species of the *Nimbadon, Plaisiodon, Neohelos* and Kolopsis clade (but see Murray, 1990b), with a division in the parametacone interpreted to have occurred subsequently in the *Kolopsis* lineage. Retraction of the mesostyle towards the cingulum in P^3 clusters species of *Neohelos* and *Kolopsis* (Murray, 1990b).

In both cladograms, the posteriorly inclined (or hooked) parastyle of P^3 in species of *Nimbadon* is regarded to be apomorphic. Only one other zygomaturine exhibits this feature — *Plaisiodon centralis*. Although species of *Nimbadon* are readily distinguished from *P. centralis* by aspects of upper premolar morphology (including in *P. centralis* the very large hypocone and the lingual crest from the parametacone linking to the protocone rather than the anterolingual cingulum) as well as by their small size, lack of a posteriorly increasing molar gradient and absence of metalophids on lower molars, sharing of the distinctively shaped parastyle may indicate an albeit distant phylogenetic relationship.

Although the three taxa described here as species of *Nimbadon* may, when better known, prove not to be monophyletic, all exhibit the distinctive crest on P^3 running lingually from the parametacone to the protocone then anteriorly to the anterolingual cingulum, a feature not previously noted in any other diprotodontoid taxa. Other features that characterise the new taxa include their small size and an M_2:M_4 length ratio which approaches 1.0. The latter are interpreted here and generally (see below) to be plesiomorphic features among diprotodontids, but they might equally be interpreted to represent apomorphic reversals within certain zygomaturine lineages.

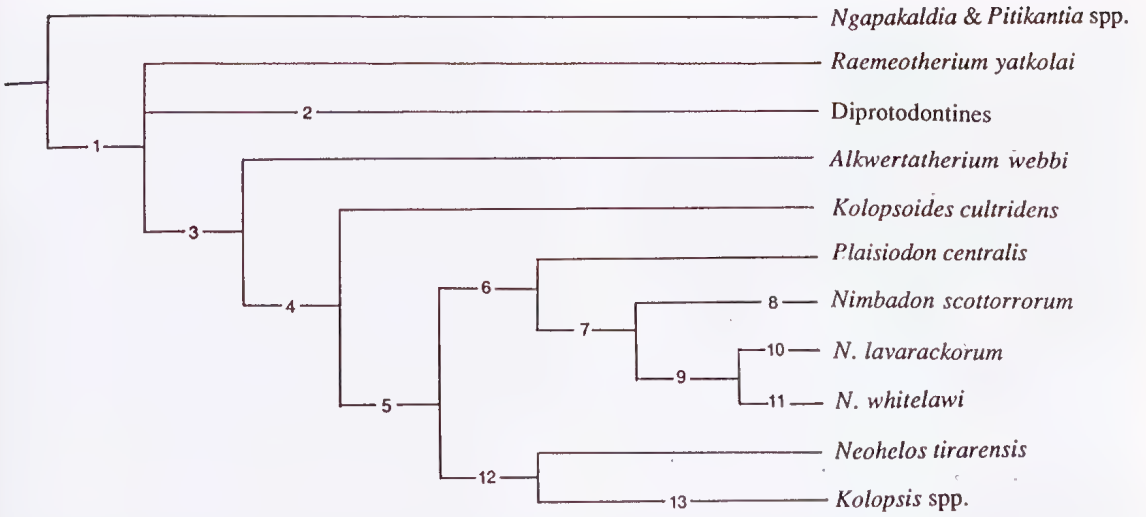

FIG. 6. A phylogenetic hypothesis of zygomaturines, broadly based on Murray's (1990b) cladistic analysis of dental characters in the Diprotodontidae. Apomorphies are as follows: 1, loss, incorporation or suppression of stylar cusps C and D with respect to the lophs on upper molars; 2, reduction of paralophid crest on M_2; 3, large parastyle on P^3 separated from parametacone by a deep cleft; 4, development of a hypocone on P^3; 5, basic proportional similarity of P^3; 6, hooked parastyle on P^3; 7, apical blade and diagonal crest on P^3; 8, shortening of P^3; 9, elongation of posterior molars (i.e. at least M3-4); 10, hypertrophy of P^3 hypocone; 11, elongation of anterior molars, i.e. M2; 12, mesostyle on P^3 retracted towards cingulum; 13, division in P^3 parametacone.

We can, however, find no pressing evidence to closely align individual species of *Nimbadon* with any previously known zygomaturine taxa.

Most zygomaturines — including species of *Zygomaturus*, *Kolopsis*, *Kolopsoides* and *Plaisiodon* — exhibit a marked increase in molar size from M2 to M4 (with an M_2-M_4 length ratio of 0.85 or less) with M5 generally decreasing in size (see also Rich, Archer & Tedford, 1978). Whether this is also true of topotypical *Neohelos tirarensis* is not known but *Neohelos* specimens from Bullock Creek and most from Riversleigh exhibit this feature.

A molar gradient of M2:M4 length approaching 1.0 is regarded by Rich, Archer & Tedford (1978) to be plesiomorphic in zygomaturines. *Raemeotherium yatkolai*, commonly considered to be the most primitive of known zygomaturines (but see Murray, 1990b, and below) and represented by a dentary, isolated lower teeth and an upper incisor from the Oligo-Miocene Namba Formation of Lake Pinpa, also has uniformly sized molars (with a ratio of M_2:M_4 length of 0.96). Palorchestids and diprotodontines variably exhibit this feature and one of the oldest known diprotodontoids, represented in the early Miocene Geilston Bay Local Fauna by a maxilla preserving part of M^2 and M^3, also has uniformly sized molars. The latter is similar in size to *R. yatkolai* but is tentatively considered by Tedford et al. (1975) to be a palorchestid. Apart from its slightly larger size, *Nimbadon lavarackorum*, the only species of the genus so far represented by lower molars, like all other zygomaturines differs from *R. yatkolai* in its reduction of anterior entocristids. *Nimbadon* species further differ from *Raemeotherium yatkolai* in being larger; in having a more massive dentary which, in transverse width, is approximately twice the width of M_3; in having less well developed cristids obliqua; relatively wider trigonids on all molars; trigonid of M_2 nearly the same width as the talonid (in contrast to *R. yatkolai* where it is markedly narrower); metaconid of M_2 as high as the protoconid and associated with a prominent, steeply inclined, swollen anterior buttress; metacristid of M_2 transversely oriented (in contrast to *R. yatkolai* where it is posterobuccally oriented); "arcuate" (rather than anteroposteriorly rectilinear) paracristid on M_2; and lophids of lower molars less occlusally concave.

It is possible that molar size gradients in zygomaturines are allometrically related to body-size, with larger animals exhibiting relatively larger posterior molars. From Oligo-Miocene deposits on Riversleigh Station, small diprotodontines have been found with M2:M4 length gradients approaching 1.0. Equally, however, the

larger of the Riversleigh species of *Nimbadon* described here (*N. scottorrorum*) appears to have been similar in overall size to at least one undescribed Riversleigh *Neohelos* that shows a marked progressive increase in molar size from M2 to M4. It seems, therefore, that the feature is not always dependent on absolute size although it may vary allometrically within lineages. In Fig. 6 it has been interpreted to be autapomorphic within various clades.

Intrageneric relationships within *Nimbadon* are not much easier to interpret. *Nimbadon whitelawi* differs from both *N. lavarackorum* and *N. scottorrorum* in its markedly more elongate upper molars (particularly with respect to *N. scottorrorum*) and relatively more anteriorly situated buccal swelling on P^3. *Nimbadon lavarackorum* differs from *N. scottorrorum* in its smaller size, less well-developed parastyle on M^3 and probably more elongate posterior upper molars and less well developed postmetacrista but more discrete metastyle on M^2. *Nimbadon scottorrorum* is larger than both *N. lavarackorum* and *N. whitelawi*, has more robust cingula on all cheek-teeth and greater parastylar development in M^{2-3} (contributing to the squared appearance of these teeth). Within *Nimbadon*, features such as the hypertrophy of the P^3 hypocone in some specimens of *N. lavarackorum* and the shortening of P^3 in *N. scottorrorum* appear to be autapomorphic features unique to those species. The most striking differences between the taxa lie in the degree of squaring (or conversely elongation) of the upper molars.

There are two quite different phylogenetic interpretations of *Nimbadon* species, depending on whether elongation (versus squaring) of the upper molars is considered to be plesiomorphic or apomorphic. Commonality would indicate squared upper molars to be plesiomorphic among diprotodontian marsupials including phalangeridans, vombatimorphians and even plesiomorphic kangaroos. However, within the Diprotodontidae the otherwise 'plesiomorphic' (i.e. simple) *Raemeotherium yatkolai* has relatively elongate lower molars and, although no uppers molars are yet known, they too would probably have been relatively elongate, using as a guide the relative proportions of the upper and lower molars of *N. lavarackorum*. It should be noted that the presumption that *R. yatkolai* is the most plesiomorphic diprotodontid is based on its simplicity. Simplicity, however, often characterises the smaller members of some diprotodontian lineages (e.g. pseudocheirids and macropodids) and all members of other lineages with ubiquitously small members (e.g. burramyids and acrobatids).

Because so few dental character systems have been found to be useful in diprotodontid systematics, polarity swings of this kind greatly influence the interpreted relationships of taxa and their biostratigraphic significance. If elongation is plesiomorphic among diprotodontoids, then *N. whitelawi* would be the most plesiomorphic of the three *Nimbadon* species. Its presence in the middle Miocene Bullock Creek Local Fauna and the presence of what would then be interpreted to be the most apomorphic in the older Fig Tree Local Fauna, would not be support for the currently understood stratigraphic relationships. If, on the other hand, elongation is interpreted to be apomorphic, then the most derived species (*N. whitelawi*) occurs in one of the younger faunas and the most plesiomorphic (*N. scottorrorum*) in the oldest of the faunas (Fig Tree).

The stratigraphic relationships of the fossil assemblages have been discussed in the Systematics section above. The Fig Tree Site occurs adjacent to units regarded to be part of Riversleigh's System B sequence as defined by Archer et al. (1989, 1991), though it may actually be basal System B or upper System A, and is interpreted to be late Oligocene to early Miocene in age. The Henk's Hollow Site occurs near the top of Riversleigh's System C sequence and the Gag Site near its base. Both lie stratigraphically above the Fig Tree level. On the basis of their positions and stage of evolution comparisons of their fossil mammals, they are interpreted to be middle Miocene in age and are probably similar in age to the Bullock Creek assemblage. The Bullock Creek Local Fauna has been interpreted by Woodburne et al. (1985), Murray (1990a) and Murray & Megirian (1990) to be middle Miocene, i.e. immediately post-Wipajiri, in age.

On balance, we consider the phylogenetic relationships of *Nimbadon* species (Fig. 6) to approximately correspond to current understanding of the relative ages of the deposits from which the specimens were obtained but conclude that for the moment at least caution is appropriate in attempts to use zygomaturines to correlate northern Australian Tertiary mammal- bearing faunas.

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DESCRIPTION OF A NEW SPECIES OF *CHAMA* FROM THE GULF OF CARPENTARIA WITH COMMENTS ON *PSEUDOCHAMA* ODHNER (MOLLUSCA: BIVALVIA: CHAMIDAE)

JOHN M. HEALY, KEVIN L. LAMPRELL AND JOHN STANISIC

Healy, J.M., Lamprell, K.L. & Stanisic, J. 1993 06 30: Description of a new species of *Chama* from the Gulf of Carpentaria with comments on *Pseudochama* Odhner (Mollusca: Bivalvia: Chamidae). *Memoirs of the Queensland Museum* **33**(1): 211-216. Brisbane. ISSN 079-8835.

A new species of Chamidae, *Chama isaacooki* sp.nov., is described from northern Australia and a key to the Australian Chamidae presented. In addition, the phenomenon of left versus right valve attachment in chamids is discussed, particularly in relation to recognition of the genus *Pseudochama* Odhner, 1917. It is concluded that the identity of valve attachment is not a reliable, sole basis for distinguishing *Pseudochama* from *Chama*.□ *Mollusca, Bivalvia, Chamidae, new species, taxonomy, Pseudochama.*

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The Chamidae (Superfamily Chamoidea) is a widespread and common family of (typically) attached heterodont bivalves, characterized by pronounced leaf-like or spinose ornamentation, coiled umbones and often marked disparity in valve size. The living chamids of Australia have most recently been treated by Lamprell & Whitehead (1992), but the family has yet to be formally revised. During our recent investigations we have had the opportunity to examine numerous specimens from the various Australian State museums as well as material from a number of large private collections. This work revealed the existence of many synonyms as well as a new species from the Arafura Sea and the Gulf of Carpentaria. In the present paper we describe this species of *Chama* and compare it to other chamids from the Indo-Pacific region. We also take the opportunity to discuss Odhner's (1917) claim that *Pseudochama* Odhner can be separated from *Chama* solely on the basis of the valve of attachment (left versus right valve).

Abbreviations used in text: AM = Australian Museum; QM = Queensland Museum; WAM = Western Australian Museum; MV = Museum of Victoria; Q = Queensland; lv = left valve; rv = right valve; pv = paired valves; L = length; H = height; W = width..

MATERIAL AND METHODS

This study is based primarily on material held in the Australian Museum (Sydney), Museum of Victoria and Queensland Museum as well as numerous specimens in private collections including the Lamprell collection. All measurements were made with Vernier callipers.

SYSTEMATICS

Superfamily CHAMOIDEA Lamarck, 1809
Family CHAMIDAE Lamarck,1809
Chama Linnaeus,1758

Type species: *Chama lazarus* Linnaeus,1758; SD Children, 1823

Chama isaacooki sp.nov.
(Figs 1-4, Table 1)

ETYMOLOGY

The name honours the memory of Isaac Cook, son of Mr Steve Cook who provided the material for this study.

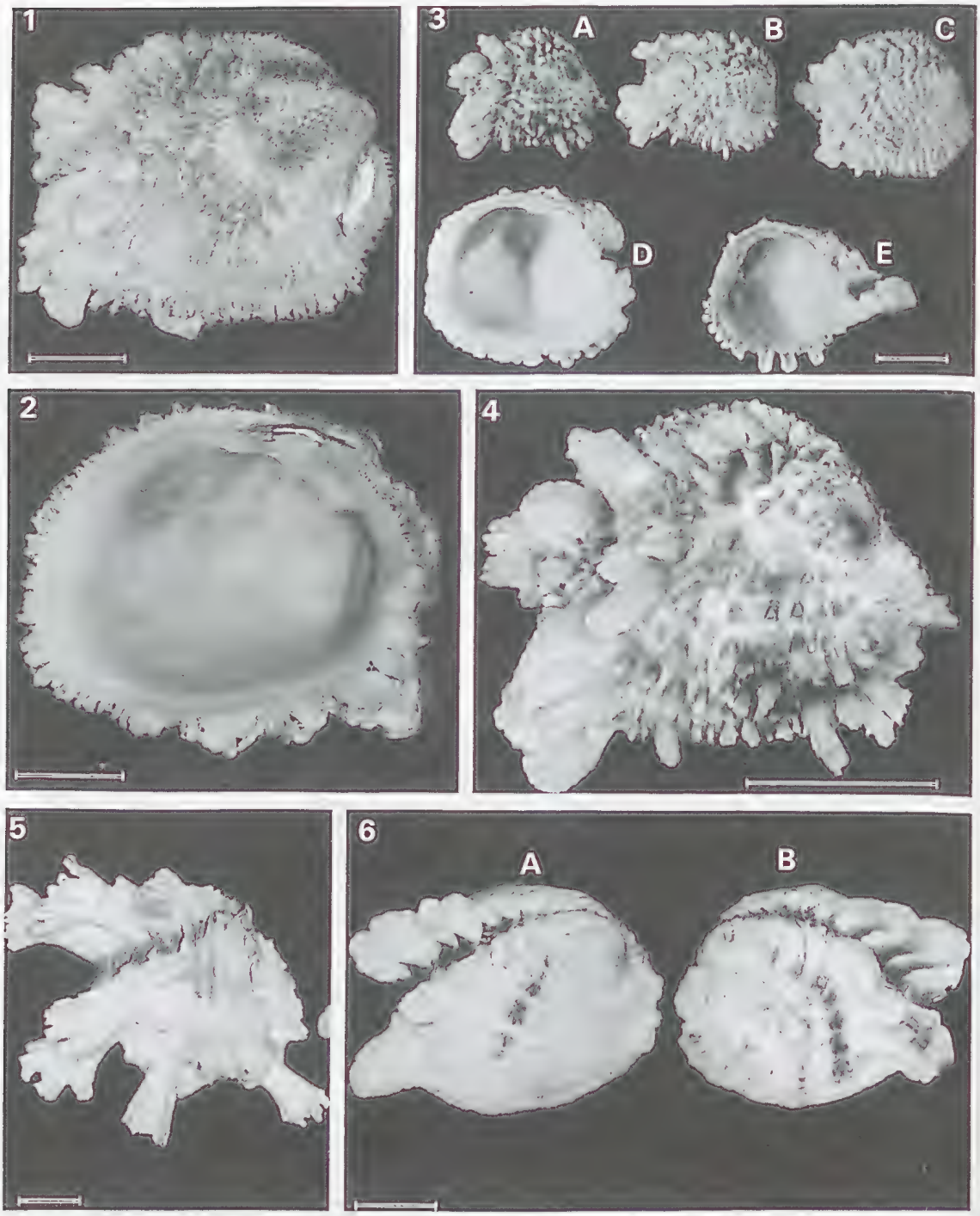
MATERIAL EXAMINED

HOLOTYPE: QMMO38412, 1 pv,Gulf of Carpentaria, 12°23.7'S, 140°41.1'E, dredged 58m, 26 Nov. 1991, S. Cook.

PARATYPES: AMC171008, 1 pv, Gulf of Carpentaria, 10°07.09'S, 141°48.36'E, dredged 47m, 1989, K Colgan; WAM83.92, lpv, Timor Sea, 12°12'S, 129°15'E, dived 37m, 17 Nov. 1989, K. Colgan; QMMO38410, QMMO38411, 2pv, Gulf of Carpentaria, 13°07'S, 141°41'E, dredged 53. 5m, 29 Nov. 1991, S. Cook.

DIAGNOSIS

Shell elongate-ovate; solid; small to moderately large; valves unequal and inequilateral; umbones prosogyrate. Externally, top (right) valve



FIGS 1-6. 1-4, *Chama isaacooki* sp.nov. 1, holotype (QMMO38412), external view of rv showing two broad bands of foliaceous spines posteriorly. 2, holotype (QMMO38412), internal view of lv showing teeth, crenulate margins and ligament. 3A,B,E, external (rv) and internal (lv) views of paratypes (A,E, WAM83.92; B, AMC171008); 3C,D, external and internal of specimen from Lamprell Collection. 4, external view of paratype (AMC171008) showing ribbed sculpture of broad spines. 5, *C. lazarus* Linnaeus, external view of rv, showing broad, foliate spines, Gove, NT. 6, *C. pulchella* Reeve. A, external view of top valve (rv), Torres Strait, NQ; B, external view of top valve (lv), Hervey Bay, SEQ. All scale bars = 10mm.

TABLE 1. Measurements (mm) of type series.

	L	H	W
Holotype: QMM038412, lpv	36.8	37.5	25.1
Paratype: AMC171008, lpv	28.5	21.4	16.5
Paratype:WAM83.92, lpv	26.9	21.1	14.6

convex, densely ornamented with rows of hollow spines radiating from the umbonal area. Spines erect or curved, ribbed and broad terminally. Posteriorly the spines become leaf-shaped and organized into two loosely defined rows, separated by smaller, vaulted spines. Externally, bottom (left) valve deeply convex and densely ornamented with vaulted spines which frequently fuse laterally to form concentric foliations. Posterior margin with small non-fused spines. Internally, margins of both valves finely crenulate. Adductor scars elongate-ovate, prominent, anterior larger than posterior. Hinge plate featuring one large, broad cardinal and one posterior (remote) lateral tooth per valve. External colouration white with orange to purple-brown blotches; spines white, purple or pink with a dark spot at the base. Internal colouration white, often with large purple blotches, particularly in young specimens. Ligament brown, elongate, parivincular.

Sample size: 8 pv. Length:height ratio — range 1:1-1:0.73; mean 1:0.86. Length:width ratio — range 1:0.75-1:0.51, mean 1:0.65.

Habitat and Distribution

Attached to living *Spondylus, Cardita* and *Crassostrea* in the Arafura Sea, Torres Strait and Gulf of Carpentaria at depths of 10 to 58m.

Remarks and Comparisons

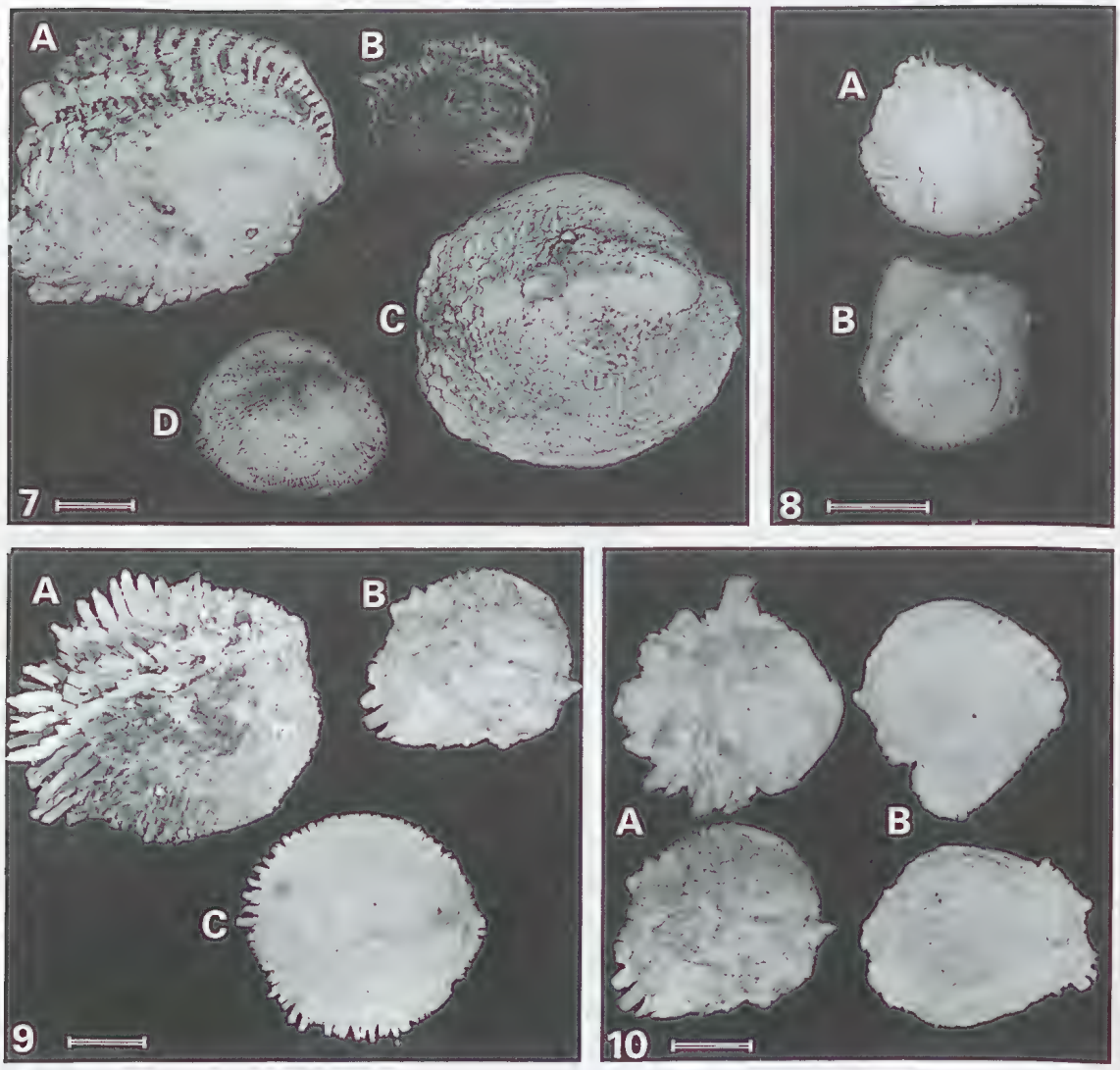
Valve ornamentation, particularly the shape and arrangement of the spines, and the consistent presence of a dark spot at the base of each spine (spot frequently absent near margin) immediately distinguish *Chama isaacooki* from others of the genus. The degree of spine preservation in exposed reef dwelling species is often poor, hence unworn juvenile material has been examined in addition to adult shells. Two prominent, posterior rows of broad spines are also present in *C. pulchella* Reeve, 1847 (Fig. 6), *C. limbula* Lamarck, 1819 (Fig. 7B), *C. fibula* Reeve, 1846 (Fig. 8) and *C. plinthota* Cox, 1927 (Fig. 7A) but not in *C. lazarus* Linnaeus, 1758 (Fig. 5), *C. pacifica* Broderip, 1834 (Fig. 9A), *C. asperella* Lamarck, 1819 (Fig. 9C) or *C. ruderalis* Lamarck, 1819 (Fig. 9B). *C. lazarus, C. pulchella* and *C. ruderalis* differ from *C. isaacooki* and other Australian chamids by totally or almost totally lacking sharp spines.

KEY TO THE AUSTRALIAN CHAMIDAE

1a. Spines broad only, often fused to form lamellae 2
Spines sharp or a mix of broad and sharp, broad spines never fused to form lamellae . . . 3
2a. Spines equally developed across valve . . . . . *C. lazarus*
Spines inequally developed across valve . . . . . *C. pulchella*
3a. Two prominent rows of broad spines dorso-posteriorly 4
Two dorso-posterior rows of spines poorly developed or not distinguishable 5
4a. Valve with strong transverse corrugations dorso-posteriorly . . . . . *C. plinthota*
Valve without strong transverse corrugations 6
5a. Spines equally developed across valve 7
Spines inequally developed across valve 8
6a. Valve margin finely crenulate. . . . *C. isaacooki*
Valve margin smooth . . . . . *C. limbula*
7a. Valve white, almost circular, strongly conex usually with rose-coloured umbone . . . . . *C. asperella*
Valve usually purple dorso-posteriorly, slightly elongate, weakly convex, umbone purple . . . . . *C. fibula*
8a. Spines raised, organized into clearly defined radial rows . . . . . *C. pacifica*
Spines prostrate, not organized into well defined rows . . . . . *C. ruderalis*

NOTES ON THE GENUS *PSEUDOCHAMA* ODHNER, 1917

Within the family Chamidae, attachment to the substrate may involve either the left valve (often referred to as the 'normal' condition) or the right valve (the 'inverse' condition) (Odhner, 1919; Cox, 1969). Early workers such as Broderip (1835) and Reeve (1846-7) indicated that both conditions may occur in the same species (for example *Chama pulchella).* Odhner (1917) disagreed and erected the genus *Psuedochama* for chamids attaching via the right valve, thereby reserving the genus *Chama* exclusively for species showing left valve attachment. He supported this division by drawing attention to differences in hinge teeth, the nepionic shell and anatomy between *Pseudochama* and *Chama* (see Odhner, 1919 for details). Although a number of recent authors have since accepted Odhner's opinion



FIGS 7-10. 7A, external view of top valve (rv) of *Chama plinthota* Cox (note strong transverse corrugations), Palm I., NEQ; 7B,C, external views of top valves (rv) of *C. limbula* Lamarck (B, immature, Fantome I., NEQ; C, One Arm Point, NWA); 7D, external view of top valve rv) of *C. fibula* Reeve, Turkey Beach, MEQ. 8A, external view of top valve (rv) of *C. fibula*, Turkey Beach, MEQ; 8B, top valve (lv) of *C. fibula*, Redcliffe, SEQ. 9A, external view of top valve (rv) of *C. pacifica* Broderip, Swain Reefs, MEQ; 9B, external view of top valve (rv) of *C. ruderalis* Lamarck, Spencer Gulf, SA; 9C, external view of top valve (rv) of *C. asperella* Lamarck, Gloucester I., MEQ. 10A, top valves (rv) of two specimens of *C. ruderalis*, Spencer Gulf, SA; 10B, top valves (lv) of two specimens of *C. ruderalis*, Spencer Gulf, SA. All scale bars = 10mm.

that the valve of attachment can be used to determine generic placement (e.g. Keen, 1969; Delsaerdt, 1986), others have maintained the earlier Broderip-Reeve view that left and right valve attachment may occur in the same species (Lamy, 1927; Cotton, 1961; Lamprell & Whitehead, 1992).

During the present study we observed both left and right valve attached specimens in *Chama pulchella, C. fibula, C. limbula* and C. *ruderalis*. Typically the left valve is favoured but in *C. limbula* the ratio of left versus right attached specimens may approach 1:1 (Cotton, 1961). Although Odhner (1919: 11,17) accepted that certain chamids showing right valve attachment and

those showing left valve attachment may appear strikingly similar to each other in external colouration, sculpture and even attached valve dentition, he maintained that such similarity was due to covergence (pp.21,22) and that right valve attachment consistently differentiated *Pseudochama* from *Chama*. He therefore held that no species of Chamidae exhibited both left and right valve fixation. Odhner stressed differences in dentition between *Pseudochama* and *Chama*, but dismissed the possibility that any similarity in the arrangement of teeth between left and right attached valves could be the result of hinge teeth 'inversion' (= transposition). According to Cox (1969: N57) transposition of the hinge teeth in chamids 'goes hand-in-hand with reversal of the valve of fixation'.

Cox cited other examples of hinge teeth transposition in living and fossil taxa and in fact recommended that the Bernardian system of tooth notation (used throughout Odhner's work) not be applied in cases of tooth transposition at least until shell ontogeny has been examined in these taxa. In fact even Odhner stated that in various species of *Chama* (sensu Odhner) the details of hinge teething may vary significantly through accentuation, suppression or addition of teeth (Odhner, 1919: 11). Yonge (1967), who made a detailed study of chamid anatomy, shell dentition and shell growth patterns, concluded that the process of cementation determined the morphology of the hinge teeth and valve profile in this family (significantly, Yonge examined both left and right valve attached specimens of *Chama pellucida* and *Pseudochama exogyra*). He supported the claim of Munier-Chalmas (1882) that free and attached valves of left valve attached specimens were mirror-images of the valves of right valve attached specimens. For this reason Yonge, like Munier-Chalmas, suggested recognizing 'free' and 'attached' valves rather than 'left' and 'right' and the application of non-Bernardian notation for Chamidae. Subsequently Yonge (1979) reverted to useage of 'left' and 'right' valves in discussing cementation in chamids (among other bivalves), but reiterated his earlier conclusion that genera within the family cannot be recognized by the valve of attachment (Yonge, 1979:100, in fact stating that 'There is no valid reason for separating the species into two genera'). By strict application of Odhner's valve of attachment rule (that is, all *Pseudochama* attach via the right valve), it would be necessary to hypothesize that left valve attached *Chama limbula, C. ruderalis, C. pulchella* and *C. fibula* each coexist with a conchologically similar, but right valve attached species of *Pseudochama*. However, in view of the fact that hinge teeth transposition has now been well demonstrated in a number of heterodont groups (Cox, 1969), and after considering Yonge's (1967, 1979) findings that cementation has had an overriding effect on hinge teeth and valve morphology in the Chamidae, we conclude that a number of chamid species are truly capable of attaching by the left or the right valve. Any observable differences in dentition between left and right 'free' valves and left and right 'attached' valves should therefore be viewed as the result of transpositional effects.

The remaining features cited by Odhner (1917, 1919) as being diagnostic of *Pseudochama* — nepionic shell sculpture and morphology and/or position of the stomach caeca and the nephridia — seem worthy of detailed investigation. It would, for example, be interesting to determine whether such features occur in right valve attached specimens of *Chama limbula, C. fibula, C. ruderalis* and *C. pulchella,* particularly the latter which Odhner (1917) named *Pseudochama similis*. Should this not be the case, then the basis for the genus *Pseudochama* would have to be reassessed.

ACKNOWLEDGEMENTS

We would like to thank Mr Steve Cook, Queensland Museum for providing specimens of *Chama isaacooki* for this study. Mr Ian Loch (Australian Museum) and Ms Sue Boyd (Museum of Victoria) provided access to collection material in their charge. Mr and Mrs Ivan Marrow (Melbourne) also allowed one of us (KL) the opportunity to examine specimens in their collection. This study was supported financially by an Australian Research Fellowship (to JH).

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A NEW CAVERNICOLOUS HARVESTMAN FROM LAVA TUBE CAVES IN TROPICAL AUSTRALIA (ARACHNIDA: OPILIONES: PHALANGODIDAE)

GLENN S. HUNT

Hunt, G.S. 1993 06 30: A new cavernicolous harvestman from lava tube caves in tropical Australia (Arachnida: Opiliones: Phalangodidae). *Memoirs of the Queensland Museum* **33**(1): 217-219. Brisbane. ISSN 0079-8835.

Zalmoxis lavacaverna sp.nov. is from lava tube caves in the Mt Surprise area, north Queensland. It is the first cave-adapted harvestman to be described from tropical Australia. Troglomorphies include depigmentation, eye reduction, and elongation of appendages and spines on pedipalp. □ *Arachnida, Opiliones, Phalangodidae, Zalmoxis lavacaverna, new species, cavernicolous, tropics, Australia.*

Glenn S. Hunt, Australian Museum, PO Box A285, Sydney South, New South Wales, 2000, Australia; 13 July, 1992.

Hitherto, no harvestmen displaying cave adaptations (troglomorphies) have been described from caves in tropical Australia. *Zalmoxis lavacaverna* sp.nov. inhabits lava tubes in inland northern Queensland and shows depigmentation, some eye regression, elongation of spines on the pedipalp and elongation of appendages.

Elsewhere in Queensland, a cave adapted species has been recorded from Hercules Cave in the limestone tower karst region of Chillagoe (Howarth, 1988). This has proved to be another species of *Zalmoxis* but its description will await the discovery of a male.

Z. lavacaverna belongs to the family Phalangodidae, a group with many cavernicolous representatives in the Northern Hemisphere (e.g. Vandel, 1965; Briggs, 1968), though these are not closely related to *Zalmoxis*. Two troglomorphic phalangodids in the genus *Chrondrobunus* have, however, been recorded from a limestone cave in New Guinea (Smith, 1980). The Phalangodidae, together with the Assamiidae, are tropical elements that replaced the older, more temperate families as Australia drifted northwards and established biological contact with Asia.

The temperate caves of southern Australia are populated by species of Triaenonychidae, predominantly the genera *Hickmanoxyomma, Holonuncia* and *Lomanella* (Hunt, 1990, 1992; Hunt and Hickman, in press). These southern caves seem to support higher numbers of cavernicolous harvestmen, though this may be a consequence of more collecting and research.

Environmental parameters and faunal diversity of the lava tube caves are discussed by Howarth (1988) and Howarth & Stone (1990). He (1988) believed the biospeleological potential of tropical caves in Australia was only just beginning to be appreciated.

Abbreviations: BMH=Bishop Museum, Hawaii; QM=Queensland Museum, Brisbane; BL=body length, BW=maximum body width, SL=scute length, CW=maximum carapace width, PFL=pedipalp femur length, FIV=femur IV length, CSL=cheliceral second segment length.

Zalmoxis lavacaverna sp.nov.
(Fig. 1)

MATERIAL EXAMINED

HOLOTYPE: QM S20731, Queensland, Collins Two-Ten Cave, Spring Creek Station, Mt Surprise, 21 Jan 1989, M. Ashe, F.G. Howarth & H. Hoch, male.

PARATYPES: QM S20732, same data, female; BMH, same data, male & female.

OTHER MATERIAL: QM S20733, Queensland, Long Shot Cave, Spring Creek Station, Mt Garnet, 20 Jan 1989, F.G. Howarth, M. Asche, H. Hoch & D. Irvin, male; QM S20734, same data, juvenile.

DIAGNOSIS

Cavernicolous. Depigmented, eyes reduced, 5 segments in tarsus IV.

DESCRIPTION

Male. Body. BL 3.10-3.15, SL 2.97-3.11, CW 1.01-1.10, BW 1.92-2.03. Depigmented, colour straw yellow to yellow-orange, appendages likewise. Anterior margin below with a process between chelicerae and between each chelicera and pedipalp, anterior margin above with 2 tubercles above each pedipalp coxa. Eyemound well developed, rising steeply a short distance behind anterior margin, armed with 1-3 tubercles, sloping less steeply posteriorly. Eye small, set low on

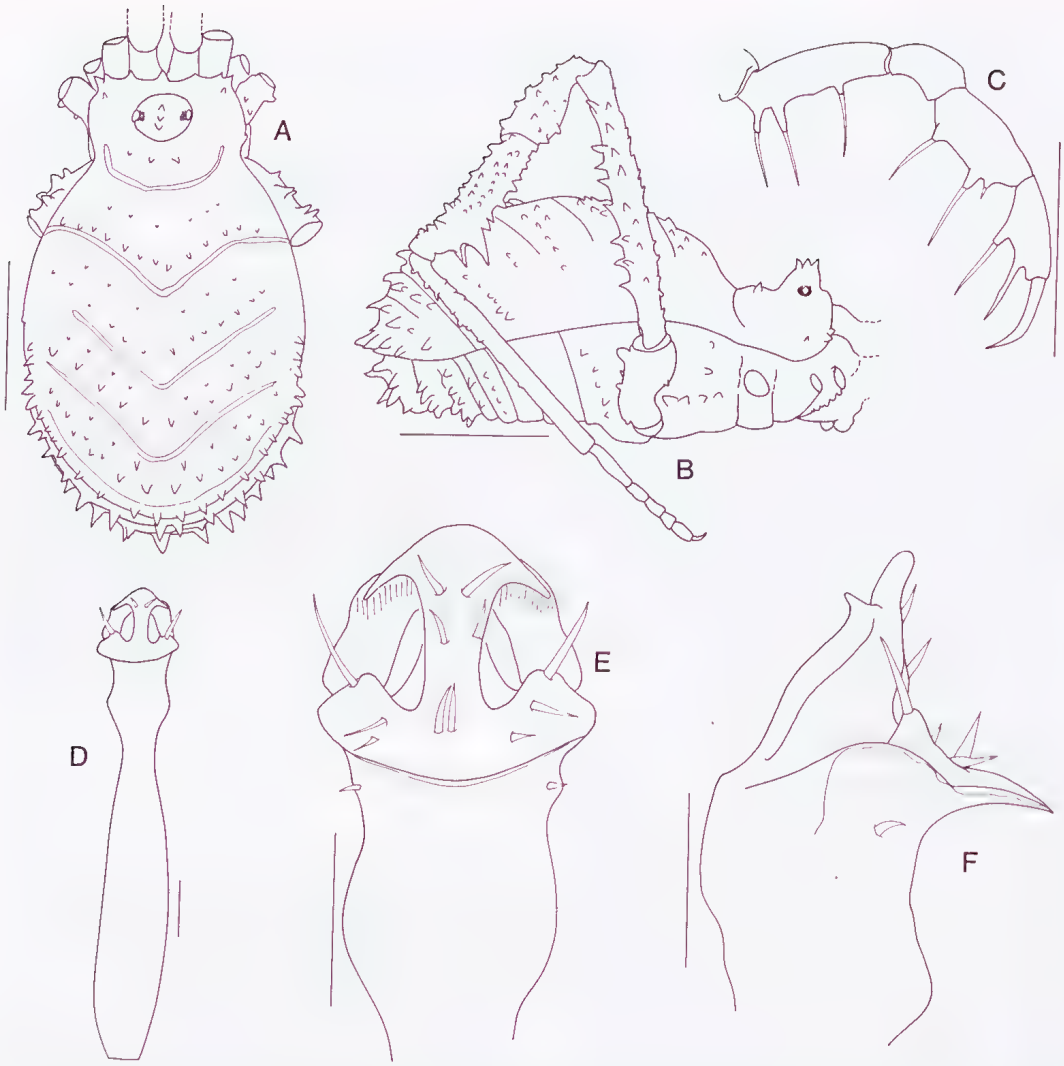

FIG. 1. *Zalmoxis lavacaverna* sp.nov., holotype male. A, body, dorsal; B, body, lateral, with leg IV; C, pedipalp, retrolateral; D, whole penis, ventral; E-F, apical part of penis, ventral and lateral. Scale bars: A-C = 1.0mm; D-F = 0.1mm.

eyemound, surrounded by small halo of pigmentation. Carapace with a few small tubercles as shown (Fig. 1A). Tergal areas 1-5 bearing a transverse row of tubercles or spines near their posterior margin, spines on TA 4 and 5 largest; TA1 - TA4 with second more anterior row composed of granules; TA5 narrow and without secondary row. The 3 free tergites each with row of strong spines; anal operculum and posterior sternites also carrying strong tubercles/spines (Fig. 1B).

Chelicera. Second segment with tiny setose granulations; CSL 0.80-0.84.

Pedipalp. PFL 0.64-0.66; femur with a two closely spaced proximoventral spines (Fig. 1C), a smaller spine ventrally at about 0.66 femur length, and a prolateral spine at about 0.75 femur length. Patella with a prolateral spines in distal half; tibia with 3 pro- and 3 retrolateral spines, most distal retrolateral spine small, remaining two retrolateral spines larger than prolateral spines. Tarsus with two pro- and two larger retrolateral spines. Setae of all spines very long. Claw subequal to tarsus.

Legs. FIV 2.20-2.34 Femora with granules enlarging to tubercles/spines on ventral surface; spines particularly strong on femur IV. Tibia IV with strong subdistal ventral spine, spines distal to it may be subequal to or stronger than other

ventral spines; otherwise patella IV to metatarsus IV coarsely tuberculate. Tarsal formula 3,5-6,5,5.

Penis. A marked ventral shelf-like projection bears 4 pairs of setae, 1 mesial pair placed close together, 2 pairs more laterally, and 1 seta inserted on each side in dorsolateral projection of shelf. 2 mesial pairs of setae are placed more distally, setae further apart than proximal mesial pair. One small pair placed below (proximal to) shelf on ventrolateral margin of penis.

Female. Differs from male in the following: much smaller, BL 2.23-2.53, SL 2.12-2.31, BW 1.54-1.57, PFL 0.53-0.57, FIV 1.52-1.54. Body and legs with more subdued spination, large distal spine on tibia IV lacking. Tarsal formula 3,5,5,5.

Variation

Spination of the eyemound varies — eyemounds with 1 spine appear more conical. The strong spine on tibia IV in males varies in strength.

Comments

On the basis of penis structure and spination of the body, *Z. lavacaverna* seems closely related to *Z. cardwellensis* Forster, 1955, which occurs in the coastal ranges directly to the east. It differs from *Z. cardwellensis* in being depigmented, having much longer appendages, a less bulbous femur IV, and 5 instead of 6 segments in tarsus IV. The female of both species is much smaller than the male. The undescribed troglomorphic species from Hercules Cave, Chillagoe, differs from *Z. lavacaverna* in having a more conical eyemound, more subdued spination of body and legs, and 6 rather than 5 segments in tarsus IV.

Etymology

The specific epithet is formed by a latinised combination of two nouns, lava and cavern, descriptive of the species habitat.

Natural History

The species was taken well inside the lava tube caves where 98-100% humidities prevail (Howarth, 1988). Howarth regarded the species as 'possibly a troglobite'. The caves support a very large troglobitic and troglophilic fauna because tree roots and bat guano provide a steady flow of energy and nutrients to the community.

Distribution

North Queensland: Long Shot and Two-Ten Caves, Collins lava tube system, Mt Surprise area. It does not seem to occur in the Bayliss lava tube, 30km to the NW, despite this cave having a rich troglobitic fauna (Howarth & Stone, 1990). This supports the view that *Z. lavacaverna* is an obligate cavernicole incapable of long dispersals across the surface.

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I thank Dr Frank Howarth, Bishop Museum, Hawaii, for making the material available to me. Dr Michael Gray, Australian Museum, commented on the manuscript and Mr Roger Springthorpe did the illustrations.

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NEW RECORD OF *LERISTA ALLANAE* (SQUAMATA: SCINCIDAE). *Memoirs of the Queensland Museum 33(1): 220. 1993:-* *Lerista allanae* (Longman,1937) was described from 3 specimens from Retro Station, near Capella. Additional material (Greer,1987; Ingram & Raven,1991) indicated a range through much of central and central eastern Queensland. However, Couper & Ingram (1992) recognised two species, the more widespread *L. colliveri* Couper & Ingram,1992 and *L. allanae* restricted to a small area between Clermont and Capella (30km in N-S direction) and 32km west of Capella. The latter was known from 9 specimens at 3 localities; it had been collected most recently in 1960 and recent searches in the same area have not added to these numbers. They concluded that the species was endangered, using the criteria of Ingram & Raven (1991:337).

In the South Australian Museum I located a specimen of *L. allanae* (R2823) from Logan Downs Station (22°23'S, 147° 56'E), 56km NE of the previously known range. It was collected by H. Womersley and registered on 16 November 1948, The collection date is not preserved with the specimen.

The specimen, an adult male (snout-vent length 72mm) with turgid testes 4.5mm long and opaque deferent ducts, agrees closely with the description of Couper & Ingram (1992) in most aspects of size and scalation, although some differences are: left hind limb missing; right hindlimb monodactyle with 6 subdigital lamellae; nuchals (paravertebral scales on nape overlapping 4 or more scales) absent; second supraocular on right side fused with right frontoparietal; superciliaries 6 in an unbroken row; infralabials 5; primary temporal present. Apparant differences in numbers of subdigital lamellae supraciliaries may reflect different reference points rather than real differences. The specimen is faded and the colour pattern only faintly discernible.

I thank Mark Hutchinson for allowing access to South Australian Museum facilities.

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Glen M. Shea, Department of Veterinary Anatomy, University of Sydney, New South Wales 2006, Australia; 20 February, 1993.

COMMON NAMES FOR QUEENSLAND FROGS

G.J. INGRAM, A.E.O. NATTRASS AND G.V. CZECHURA

Ingram, G.J., Nattrass, A.E.O. & Czechura, G.V. 1993 06 30: Common names for Queensland frogs. *Memoirs of the Queensland Museum* 33(1): 221-224. Brisbane. ISSN 0079-8835.

In Queensland, there has been a great increase in public interest in frogs. However, communication about frogs has been hampered by the lack of common, or English, names for the species. This checklist attempts to rectify the problem of communication by allocating a distinct common name to each species. The names are based on our experience of the frogs in the wild and familiarity with common names already in use. □ *Anura, frog, common name, nomenclature, checklist, Queensland.*

Glen Ingram & Greg Czechura, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; Ric Nattrass, 25 Warwick Court, Bellbird Park, Queensland 4300, Australia; 29 April, 1993.

In recent years there has been a great increase in public interest and concern regarding Queensland's native frogs. Several amateur societies have now been established throughout the State to watch, study or restore populations of frogs. Disappearance and possible extinction of several species in the wild and wider declines of others as a result of urban-sprawl have catalysed growing public fascination. 'Frog experts' are now in great demand to provide information about Queensland's frog fauna to both the public and media. However, scientists and naturalists are experiencing difficulties in communication because most frogs are only known by their scientific names: the media and public are reluctant to use these.

Some attempts have been made to introduce common, or English, names for popular usage (Moore, 1961; Clyne, 1969; Barker & Grigg, 1977; Ingram, 1983; Cogger, 1992 & earlier editions; Tyler, 1992). Not all of these efforts were comprehensive or not all the suggested names were adopted. Most suggestions have been based on literal translations of the latin nomenclature and this has often led to common names that are inappropriate, unwieldy or obscure. For example, *Litoria rubella* has been assigned the names 'Purple Treefrog' and 'Red-purple Treefrog' even though very few individuals are purple. And, inappropriately, it has also been called 'Desert Treefrog' even though it is commonly found in habitats other than desert. For many general users, the names recommended by scientists simply lack the 'colour' and 'descriptiveness' of the common names assigned to, for example, hummingbirds as in Sibley & Monroe (1990).

The following list — which has been developed from field experience, common names already in use and discussions with interested parties — attempts to redress this imbalance by allocating a distinct common name to each species that occurs in Queensland. Common names should reflect some distinctive attribute of a taxon, or the place where they live, so that it is appropriate in most, if not all, contexts. As well, it should not create a misleading preconception of appearance. Furthermore, we feel it is desirable that designations using 'toad' only refer to the introduced *Bufo marinus*. Thus species of *Uperoleia* are herein referred to as 'gungans' from an aboriginal name (see Ingram & Corben, 1975) and not as 'toadlets'. 'Toadlet' should only be used to describe juvenile *B. marinus*.

In choosing and framing English names, we have followed the principles of Royal Australasian Ornithologists Union (R.A.O.U., 1978). Scientific names follow Ingram (1991) with addition of *U. altissima* Davies, Watson, McDonald, Trenerry & Werren, 1993.

CHECKLIST OF QUEENSLAND FROGS

TOADS
BUFONIDAE

Bufo Laurenti, 1768
CANE TOAD *B. marinus* (Linnaeus, 1758)

TREEFROGS AND RELATIVES
HYLIDAE

Cyclorana Steindachner, 1867
NORTHERN SNAPPING-FROG *C. australis* (Gray, 1842)
SUPERB COLLARED-FROG *C. brevipes* (Peters, 1871)
DESERT COLLARED-FROG *C. cultripes* Parker, 1940
WESTERN COLLARED-FROG *C. maini* Tyler & Martin, 1977

LITTLE COLLARED-FROG *C. manya* Van Beurden & McDonald, 1980
EASTERN SNAPPING-FROG *C. novaehollandiae* Steindachner, 1867
WATER-HOLDING FROG *C. platycephalus* (Günther, 1873)

Litoria Tschudi, 1838
GREENSTRIPE FROG *L. alboguttatus* (Günther, 1867)
NORTHERN SEDGEFROG *L. bicolor* (Gray, 1842)
GREEN-THIGHED FROG *L. brevipalmata* Tyler, Martin & Watson, 1972
GREEN TREEFROG *L. caerulea* (White, 1790)
SOUTHERN ORANGE-EYED TREEFROG *L. chloris* (Boulenger, 1893)
COOLOOLA SEDGEFROG *L. cooloolensis* Liem, 1974
SANDSTONE FROG *L. coplandi* (Tyler, 1968)
NORTHERN WATERFROG *L. dahlii* (Boulenger, 1896)
BLEATING TREEFROG *L. dentata* (Keferstein, 1868)
ELECTRIC TREEFROG *L. electrica* Ingram & Corben, 1990
EASTERN SEDGEFROG *L. fallax* (Peters, 1880)
WALLUM ROCKETFROG *L. freycineti* Tschudi, 1838
GREEN-EYED TREEFROG *L. genimaculata* (Horst, 1883)
GRACEFUL TREEFROG *L. gracilenta* (Peters, 1869)
BUMPY ROCKETFROG *L. inermis* (Peters, 1868)
WHITE-LIPPED TREEFROG *L. infrafrenata* (Günther, 1867)
BROAD-PALMED ROCKETFROG *L. latopalmata* Günther, 1867
STONY-CREEK FROG *L. lesueuri* (Duméril & Bibron, 1841)
SCRUB ROCKETFROG *L. longirostris* Tyler & Davies, 1977
ARMOURED MISTFROG *L. lorica* Davies & McDonald, 1979
PYGMY ROCKETFROG *L. microbelos* (Cogger, 1966)
WATERFALL FROG *L. nannotis* (Andersson, 1916)
STRIPED ROCKETFROG *L. nasuta* (Gray, 1842)
TAWNY ROCKETFROG *L. nigrofrenata* (Günther, 1867)
MOUNTAIN MISTFROG *L. nyakalensis* Liem, 1974
WALLUM SEDGEFROG *L. olongburensis* Liem & Ingram, 1977
PEACH-SIDED ROCKETFROG *L. pallida* Davies, Martin & Watson, 1983
CASCADE TREEFROG *L. pearsoniana* (Copland, 1961)
EMERALD-SPOTTED TREEFROG *L. peronii* (Tschudi, 1838)
WHIRRING TREEFROG *L. revelata* Ingram, Corben & Hosmer, 1982
COMMON MISTFROG *L. rheocola* Liem, 1974
RED-EYED TREEFROG *L. rothii* (de Vis, 1884)
NAKED TREEFROG *L. rubella* (Gray, 1842)
NEW ENGLAND TREEFROG *L. subglandulosa* Tyler & Anstis, 1983
BLACK-SHINNED ROCKETFROG *L. tornieri* (Nieden, 1923)
LAUGHING TREEFROG *L. tyleri* Martin, Watson, Gartside, Littlejohn & Loftus-Hills, 1979
WHISTLING TREEFROG *L. verreauxii* (Duméril, 1853)
GIANT ROCKETFROG *L. wotjulumensis* (Copland, 1957)
NORTHERN ORANGE-EYED TREEFROG *L. xanthomera* Davies, McDonald & Adams, 1986

Nyctimystes Stejneger, 1916
AUSTRALIAN LACE-LID *N. dayi* (Günther, 1897)

NARROW-MOUTHED FROGS MICROHYLIDAE

Cophixalus Boettger, 1892
WINDSOR NURSERY-FROG *C. bombiens* Zweifel, 1985
TAPPING NURSERY-FROG *C. concinnus* Tyler & Davies, 1979
NORTHERN NURSERY-FROG *C. crepitans* Zweifel, 1985
BLOOMFIELD NURSERY-FROG *C. exiguus* Zweifel & Parker, 1969
PIPPING NURSERY-FROG *C. hosmeri* Zweifel, 1985
BUZZING NURSERY-FROG *C. infacetus* Zweifel, 1985
SOUTHERN NURSERY-FROG *C. mcdonaldi* Zweifel, 1985
TANGERINE NURSERY-FROG *C. neglectus* Zweifel, 19623
COMMON NURSERY-FROG *C. ornatus* (Fry, 1912)
CAPE YORK NURSERY-FROG *C. peninsularis* Zweifel, 1985
BOULDER NURSERY-FROG *C. saxatilis* Zweifel & Parker, 1977

Sphenophryne Peters & Doria, 1878
CRICKET CHIRPER *S. fryi* Zweifel, 1962
SHRILL CHIRPER *S. gracilipes* (Fry, 1912)
WHITE-BROWED CHIRPER *S. pluvialis* Zweifel, 1965
PEALING CHIRPER *S. robusta* (Fry, 1912)

PARENTAL-CARE FROGS AND RELATIVES MYOBATRACHIDAE

Adelotus Ogilby, 1907
TUSKED FROG *A. brevis* (Günther, 1863)

Assa Tyler, 1976
AUSTRALIAN MARSUPIAL FROG *A. darlingtoni* (Loveridge, 1933)

Crinia Tschudi, 1838
CHIRPING FROGLET *C. deserticola* (Liem & Ingram, 1977)
BEEPING FROGLET *C. parinsignifera* Main, 1957
TORRID FROGLET *C. remota* (Tyler & Parker, 1974)
CLICKING FROGLET *C. signifera* (Girard, 1853)
WALLUM FROGLET *C. tinnula* Straughan & Main, 1966

Kyarranus Moore, 1958
RED-AND-YELLOW MOUNTAIN-FROG *K. kundagungan* Ingram & Corben, 1975
MASKED MOUNTAIN-FROG *K. loveridgei* (Parker, 1940)

Lechriodus Boulenger, 1882
BLACK-SOLED FROG *L. fletcheri* (Boulenger, 1890)

Limnodynastes Fitzinger, 1843
MARBLED FROG *L. convexiusculus* (Macleay, 1877)
GREY-BELLIED POBBLEBONK *L. dumerilii* Peters, 1863
BARKING FROG *L. fletcheri* Boulenger, 1888
ORNATE BURROWING-FROG *L. ornatus* (Gray, 1842)
STRIPED MARSHFROG *L. peronii* (Duméril & Bibron, 1841)
SALMON-STRIPED FROG *L. salmini* Steindachner, 1867
SPOTTED MARSHFROG *L. tasmaniensis* Günther, 1858
SCARLET-SIDED POBBLEBONK *L. terraereginae* Fry, 1915

Mixophyes Günther, 1864
GREAT BARRED-FROG *M. fasciolatus* Günther, 1864
FLEAY'S BARRED-FROG *M. fleayi* Corben & Ingram, 1987
GIANT BARRED-FROG *M. iteratus* Straughan, 1968
NORTHERN BARRED-FROG *M. schevilli* Loveridge, 1933

Neobatrachus Peters, 1863
RATTLING METAL-EYED FROG *N. aquilonius* Tyler, Davies & Martin, 1981
TRILLING METAL-EYED FROG *N. centralis* (Parker, 1940)
EASTERN METAL-EYED FROG *N. sudelli* (Lamb, 1911)

Notaden Günther, 1873
HOLY CROSS FROG *N. bennettii* Günther, 1873
BROWN ORBFROG *N. melanoscaphus* Hosmer, 1962
RUBY-SPOTTED ORBFROG *N. nichollsi* Parker, 1949

Pseudophryne Fitzinger, 1843
RED-BACKED BROODFROG *P. coriacea* Keferstein, 1868
GREAT BROWN BROODFROG *P. major* Parker, 1940

Rheobatrachus Liem, 1973
SOUTHERN PLATYPUSFROG *R. silus* Liem, 1973
NORTHERN PLATYPUSFROG *R. vitellinus* Mahony, Tyler & Davies, 1984

Taudactylus Straughan & Lee, 1966
SHARP-SNOUTED DAYFROG *T. acutirostris* (Andersson, 1916)
SOUTHERN DAYFROG *T. diurnus* Straughan & Lee, 1966
EUNGELLA DAYFROG *T. eungellensis* Liem & Hosmer, 1973
EUNGELLA TINKERFROG *T. liemi* Ingram, 1980
KROOMBIT TINKERFROG *T. pleione* Czechura, 1986
NORTHERN TINKERFROG *T. rheophilus* Liem & Hosmer, 1973

Uperoleia Gray, 1841
TABLELAND GUNGAN *U. altissima* Davies, Watson, McDonald, Trenerry & Werren, 1993
DESERT GUNGAN *U. capitulata* Davies, McDonald & Corben, 1986
SANDY GUNGAN *U. fusca* Davies, McDonald & Corben, 1986
FLOODPLAIN GUNGAN *U. inundata* Tyler, Davies & Martin, 1981
EASTERN GUNGAN *U. laevigata* Keferstein, 1867
STONEMASON GUNGAN *U. lithomoda* Tyler, Davies & Martin, 1981
RED-SPECKLED GUNGAN *U. littlejohni* Davies, McDonald & Corben, 1986
TORRES GUNGAN *U. mimula* Davies, McDonald & Corben, 1986
CHUBBY GUNGAN *U. rugosa* (Andersson, 1916)
ORANGE-SHOULDERED GUNGAN *U. trachyderma* Tyler, Davies & Martin, 1981

TRUE FROGS
RANIDAE

Rana Linnaeus, 1758
AUSTRALIAN BULLFROG *R. daemeli* Steindachner, 1868

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SPERMATOLOGICAL EVIDENCE FOR THE TAXONOMIC STATUS OF *TRAPEZIA* (CRUSTACEA: BRACHYURA: HETEROTREMATA)

B.G.M. JAMIESON

Jamieson, B.G.M. 1991 06 30: Spermatological evidence for the taxonomic status of *Trapezia* (Crustacea: Brachyura: Heterotremata). *Memoirs of the Queensland Museum* 33(1): 225-234. Brisbane. ISSN 0079-8835.

Features of the spermatozoon of *Trapezia* which are general for heterotremes and endorse its inclusion in the Heterotremata are: extension of the subacrosomal chamber almost to the anterior apex of the sperm; division of the acrosome contents into inner and outer zones; presence of an acrosomal ray zone at the periphery of the inner acrosomal zone; and presence of a thickened ring where the acrosomal capsule surrounds the base of the subacrosomal chamber. A feature shared with 'higher' heterotremes is the restriction of cytoplasm to the periacrosomal region, the arms being nuclear only; and loss of a posterior median process, containing chromatin, which is present in raninids and majids. Additional features which *Trapezia* shares with the Xanthidae (exemplified by Xanthinae and Chlorodiinae) and Panopeidae (exemplified by *Eurytium*) include the structure of the perforatorium, tapering anteriad, with a fibrous core; and extension of the chromatin around the operculum, leaving only a raised central area of this exposed. Peculiar features of xanthids (Xanthinae, Chlorodiinae) and panopaeids which separate them from all other heterotremes, including *Trapezia*, are the dense 'xanthid ring' around the base of the subacrosomal chamber and, in xanthids, the additional peripheral zone outside the outer acrosomal zone. Presence of a presumed derivative of the xanthid ring in thoracotremes indicates that the Xanthidae s. strict. and panopaeids are near the base of the Thoracotremata and absence of the ring in *Trapezia* suggests that it (in the Trapeziidae) is the plesiomorphic sister- or neighbouring-taxon of the xanthid-panopaeid assemblage. An apomorphy of *Trapezia* is restriction of the acrosome ray zone to an annulus around the anterior region of the perforatorium. Presence of the ring or its derivatives indicates that although the xanthids, panopaeids, and such thoracotremes form a monophyletic group, the Xanthoidea is a paraphyletic group. □ *Crustacea, phylogeny, spermatozoa, ultrastructure, Trapezia, Pilodius, Eurytium, Mictyris.*

B.G.M. Jamieson, Zoology Department, University of Queensland, Queensland 4072, Australia; Honorary Associate, Queensland Museum; 7 May, 1992.

Trapezia Latreille, 1825, is a genus of heterotreme crabs, the species of which are obligate symbionts of corals (Abele & Felgenhauer, 1982). The 'trapézides' of A. Milne Edwards, 1862, were given subfamilial rank, as the Trapeziinae, by Miers (1886) in the family Xanthidae of Macleay, 1838. This allocation of *Trapezia* was widely accepted. However, Guinot (1978) revived Ortmann's (1893) idea, subsequently abandoned, that a family Trapeziidae should be recognised. Within her Xanthoidea, Guinot (1978: 275) considered the Trapeziidae Miers to be a distinctive family equal in rank to the Xanthidae, and other xanthoid families (the Carpiliidae, Menippidae, Platyxanthidae, Pilumnidae, Panopeidae and Geryonidae), a view supported by specialists on the genus *Trapezia* (e.g. Clark & Galil, 1988).

Despite objections that classification on larval characters conflicts with that on adult characters (Gurney, 1938; Lebour, 1944), studies of larval development have been considered to confirm relationship of *Trapezia* with other xanthoid genera (Hyman, 1925; Wear, 1970; Rice, 1980; Martin, 1984). The classifications of Hyman (1925) and Wear (1970) suggested a special relationship of *Trapezia* to menippines and pilumnines (Menippidae and Pilumnidae sensu Guinot, 1978). Nevertheless, Guinot (unpublished) considers that the distinctive morphology of *Trapezia* may justify recognition of a distinct superfamily Trapezoidea.

The present study examines the ultrastructure of the spermatozoa of *Trapezia coerulea* with a view to providing evidence of its relationships. For comparative purposes, micrographs are included of the sperm of the xanthid *Pilodius areolatus* and the thoracotreme *Mictyris longicarpus* (Mictyridae) and brief reference (in the Discussion) is made to the sperm of the panopaeid *Eurytium limosum* (Say) (Jamieson & Abele, unpublished). Published descriptions of xanthoid sperm are limited to a brief description for *Menippe mercenaria* (Menippinae) by Brown

(1966) in an unpublished doctoral thesis; a diagram of the sperm of *Atergatis floridus* (Linnaeus) in a discussion of malacostracan phylogeny by Jamieson (1989c); detailed description of the sperm of *Atergatis floridus* (Xanthidae, Zosiminae), *Etisus laevimanus* Randall (Xanthidae, Etisinae), *Liagore rubromaculata* De Haan (Carpiliidae, incertae sedis) and *Pilodius areolatus* (H. Milne-Edwards) (Xanthidae, Chlorodiinae) by Jamieson (1989a); brief mention of *Eurypanopeus depressus* (Smith) and an SEM micrograph for *Eurytium limosum* (Say) (both Panopeidae) by Felgenhauer & Abele (1990) and a description for *Geryon fenneri* and *G. quinquedens* (Geryonidae), by Hinsch (1988). It is unfortunate that no descriptions of spermatozoal ultrastructure exist for Pilumnidae and that the brief description for *Menippe mercenaria* by Brown (1966) in an unpublished doctoral thesis does not give sufficient detail for purposes of comparison, in view of the supposed relationship of these to *Trapezia*.

MATERIAL AND METHODS

Species examined for sperm ultrastructure are: *Trapezia coerulea* Rüppell, from Heron Island, Great Barrier Reef; the xanthid *Pilodius areolatus* (H. Milne-Edwards), from One Tree Island, Great Barrier Reef; the panopaeid *Eurytium limosum* (Say) (see Discussion only) from the vicinity of Talahassee, Florida, USA; and the thoracotreme *Mictyris longicarpus* Latreille (Mictyridae), from Moreton Bay, Queensland. The specimen of *Trapezia* used has been lodged in the collections of the Queensland Museum.

Small portions of testes of were fixed in 3% glutaraldehyde in 0.1M phosphate buffer (pH 7.4), with 6% sucrose, at 4°C, washed in buffer, post-fixed for 80 min in similarly buffered 1% osmium tetroxide, washed in buffer, dehydrated through an ascending ethanol series, and infiltrated and embedded in Spurr's epoxyresin. Thin sections were cut with a diamond knife on an LKB 2128 UM IV ultrotome, collected on carbon stabilised colloidin-coated 200 mesh copper grids, and stained by the Daddow method: for 0.5 min in Reynolds' lead citrate, 1 min in 6% aqueous uranyl acetate and a further 0.5 min in lead citrate, before rinsing in distilled water. Specimens were examined with a Hitachi 300 and a Jeol 100S transmission electron microscope operated at 80kV and 60kV respectively.

RESULTS AND COMPARATIVE REMARKS

The terminology adopted by Jamieson (1989a,b, 1991) will be employed in this account with the modification that the inner zone of the acrosome and the acrosome ray zone will be recognised as distinct layers, rather than being combined under the term inner dense zone. This modification of terminology will accommodate the condition in paguroid anomurans where the acrosome ray zone may form the widest layer of the acrosome. Although in Brachyura the acrosome ray zone is sometimes poorly delimited from or forms part of an inner dense zone, the two layers will therefore be recognised as the 'inner acrosomal zone' and the 'acrosome ray zone'. To minimise repetition of data from *Trapezia* in the Discussion, some comparison with archaeobrachyuran and other heterotreme crabs will be made in the Results. Comparison with thoracotremes will chiefly be reserved to the Discussion.

GENERAL MORPHOLOGY

The spermatozoon of *Trapezia coerulea* is illustrated from transmission electron microscopy in a line drawing (Fig. 1) and in micrographs (Fig. 2). For comparison with a xanthid and a thoracotreme, these are illustrated by micrographs of the sperm of *Pilodius areolatus* (Fig. 3) and the thoracotreme *Mictyris longicarpus* (Fig. 4).

The spermatozoon of *Trapezia coerulea* (Fig. 1) is spheroidal but slightly depressed anteroposteriorly and, like all decapod sperm, lacks a flagellum (Fig. 2B). This simple form is modified by the presence of broadly based lateral projections or 'arms'. From light micrographs, there are four arms, each with a length considerably surpassing the diameter of the sperm body. A plesiomorphic, chromatin-containing 'posterior median process', seen in *Ranina* and some majids, is absent. As is usual for brachyurans, the nucleus consists of diffuse, fibrous chromatin, and forms a cup surrounding the acrosome, a thin layer of cytoplasm intervening between nucleus and acrosome. The cytoplasm contains sparse mitochondria, some membranous (lamellar) structures of probable mitochondrial origin and, basal to the perforatorium, the two centrioles (Figs 2B,C,D).

ACROSOME

The subspheroidal core of the *Trapezia* spermatozoon consists entirely of the complex

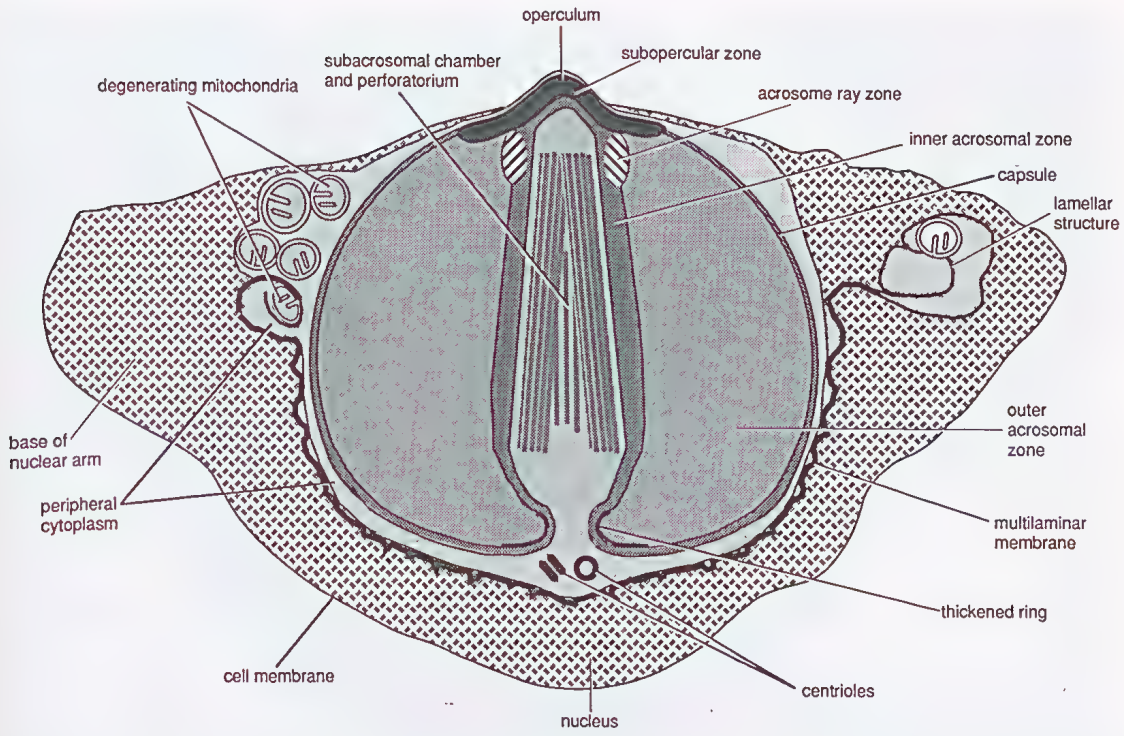


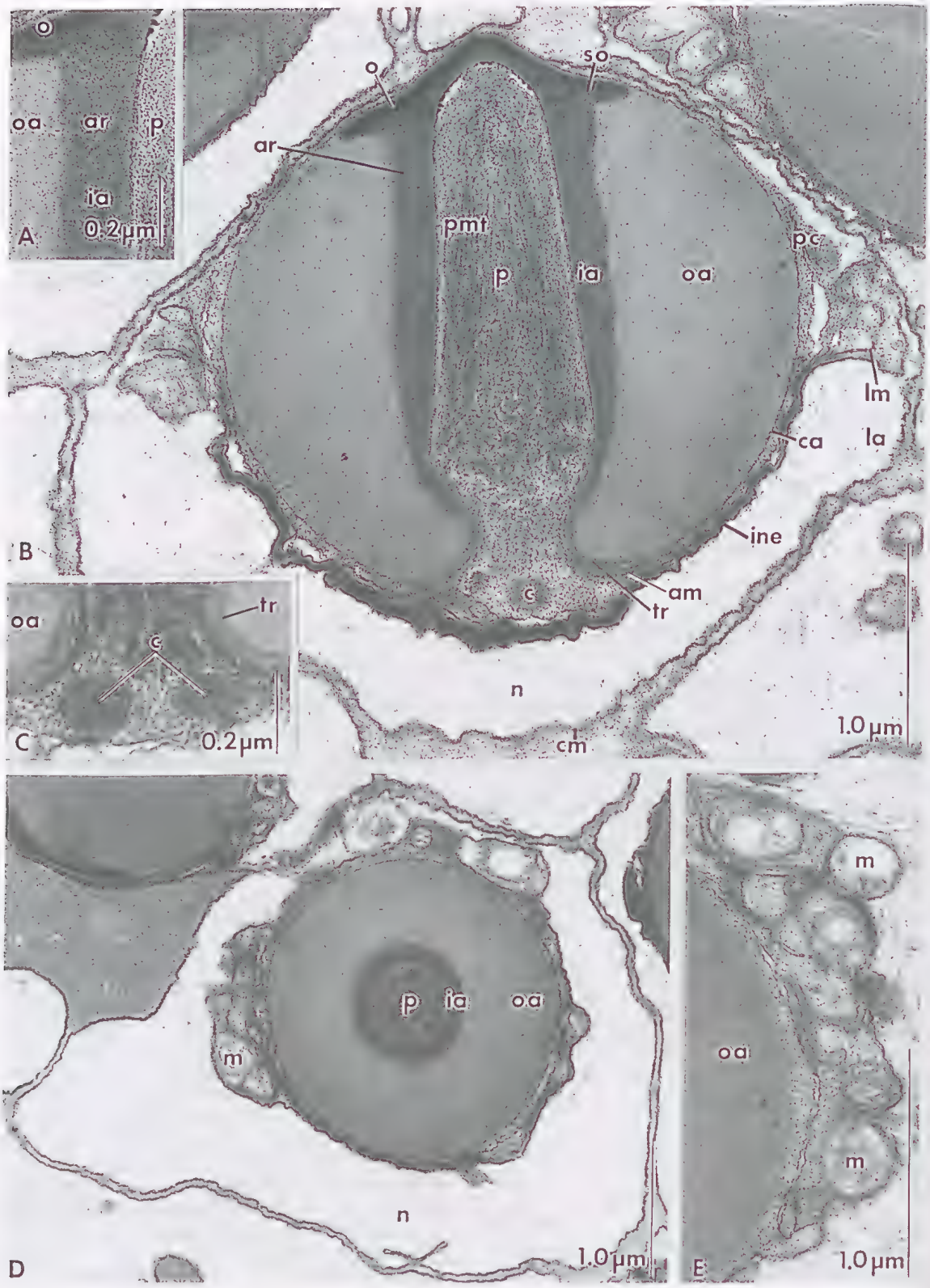
FIG. 1. *Trapezia coerulea*. Diagrammatic representation of a longitudinal sagittal section of the spermatozoon.

acrosome. This is composed of a number of components identifiable with, and presumably homologous with, those described for other higher brachyuran sperm (Jamieson, 1989a,b, 1991).

The acrosome (Figs 2B,D) is invested by an acrosomal membrane underlain by an electron dense sheath, the 'capsule'. The length of the acrosome, from the apex of the operculum to the base of the thickened ring, is 2.4-2.9μm (mean of 3 = 2.6μm); the width is 2.6-3.0μm (mean of 3 = 2.8μm). The acrosomal membrane is separated by a very thin, pale layer, from the capsule and, like the capsule, is invaginated at the posterior pole to cover a columnar subacrosomal chamber (Fig. 2B), the contents of which are the perforatorium. The anterior tip of this chamber extends almost to the anterior apex of the sperm. As in most other crabs, this central, subacrosomal axis of the acrosome is surrounded by a wide electron dense sheath, the 'inner acrosomal zone' (Figs 2B, D). Unlike xanthoids for which sperm descriptions are sufficiently detailed (*Pilodius areolatus*, Fig. 3, *Atergatis floridus*, *Etisus laevimanus* and *Liagore rubromaculata*) there is no differentiation of the posterior part of the inner acrosomal zone as an electron dense prominent annulus, the 'xanthid ring'.

As in xanthids of the Xanthinae and Chlorodiinae, but in this case in the absence of the xanthid ring, the inner acrosomal zone in *Trapezia* is surrounded by an 'acrosome ray zone' (Fig. 2A,B) seen also in other heterotremes and in paguroid anomurans (Jamieson, 1991). In xanthids (Fig. 3), the dorippid *Neodorippe*, and portunids, the acrosome ray zone extends for much of the length of the inner layer (being especially wide in portunids), but in *Trapezia* (Fig. 2A,B) it is limited to a slightly convex annulus restricted to, and embedded in, the anterior region of the inner acrosomal zone, from which it is poorly demarcated.

In *Trapezia* as in xanthids, portunids and other heterotremes, the inner acrosomal zone, with the ray zone, is in turn surrounded by a broad layer, the outer acrosomal zone (Figs 2B,D). In *Trapezia*, as in heterotremes excepting xanthids, this zone is the only additional concentric layer and continues to the capsule. In xanthids, in contrast, it is differentiated into an outer dense zone, next to the inner acrosomal zone and ray zone, and a further, peripheral zone (Fig. 3). The external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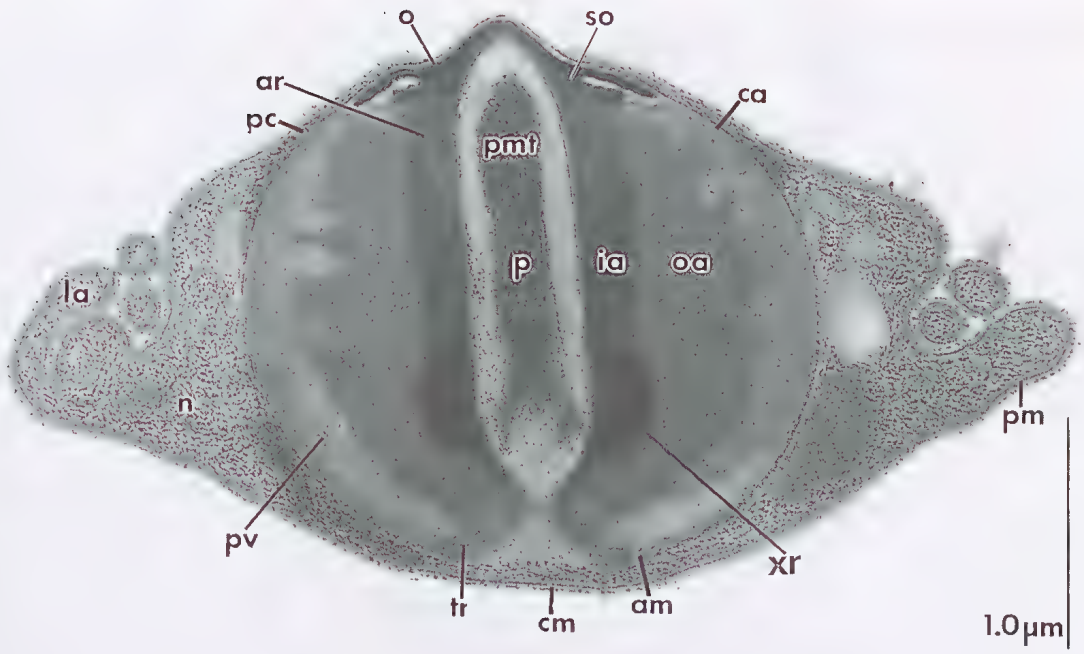


FIG. 3. Transmission electron micrograph of a longitudinal sagittal section of the spermatozoon of the xanthid *Pilodius areolatus*. Abbreviations: am = acrosome membrane; ar = acrosomal rays; ca = capsule; cm = cell membrane; ia = inner acrosomal zone; la = base of lateral arm; n = nucleus; o = operculum; oa = outer acrosomal zone; p = perforatorium; pc = vestigial periacrosomal cytoplasm; pmt = microtubules of perforatorium; so = subopercular zone; tr = thickened ring; xr = xanthid ring.

margin of the outer dense zone peculiar to xanthids is ragged and deeply dissected (*Atergatis* and *Pilodius*) or slightly crenulated (*Etisus*) or almost smooth (*Liagore*).

At the anterior pole of the *Trapezia* acrosome, as in all other brachyurans and paguroids with the doubtful exception of *Pagurus bernhardus* (see Chevaillier, 1968), there is a dense caplike structure, the operculum (Fig. 2B), 1.3- 1.5µm wide (mean of 3 = 1.4µm). As in *Portunus*, the operculum is imperforate whereas in *Ranina* and the majid *Menaetheus monoceros* it is perforate (see Jamieson, 1991), although in some individual xanthid sperm it appears weakened apically (it is also perforate but is closed by an apical button in most of the investigated thoracotremes, Fig. 4A, see Discussion).

Below the operculum, as in many other crabs, a further, caplike structure of moderately electron dense material, the subopercular zone, separates the operculum and adjacent region of the capsule from the summit of the inner acrosomal zone and acrosome ray zone (Fig. 2B). In *Trapezia*, as in xanthids, the operculum extends laterally slightly beyond the acrosome ray zone. In contrast the operculum is limited in *Calappa* to the width of the ray zone while in portunids and dorippids it is more extensive as it also caps the outer acrosomal zone (see Jamieson, 1991).

At the opposite, posterior, pole the capsule is perforated by invagination of the acrosome membrane and capsule as a narrow orifice which opens into the columnar subacrosomal chamber. Unlike the *Ranina* sperm but like that of *Calappa*, portunids, *Neodorippe* and xanthids, a thickening of

FIG. 2. *Trapezia coerulea*. Transmission electron micrographs of the spermatozoon. A. Detail of acrosome ray zone. B. Longitudinal sagittal section. C. Detail of centriolar region. D. Transverse section shortly below the equator of the acrosome. E. Detail of the cytoplasmic layer in transverse section, showing mitochondria in various stages of degeneration. Abbreviations: am = acrosome membrane; ar = acrosomal rays; c = centriole(s); ca = capsule; cm = cell membrane; ia = inner acrosomal zone; ine = multilayered inner nuclear envelope; la = base of lateral arm; lm = contorted (lamellar) membranes; m = degenerating mitochondrion; n = nucleus; o = operculum; oa = outer acrosomal zone; p = perforatorium; pc = vestigial periacrosomal cytoplasm; pmt = microtubules of perforatorium; so = subopercular zone; tr = thickened ring.

the capsule forms a 'thickened ring' on each side of the subacrosomal invagination (Fig. 2B).

Subacrosomal Region

In *Trapezia*, as in xanthids and other heterotreme (and thoracotreme) Brachyura, the subacrosomal material consists of a highly differentiated stout perforatorium that extends from the posterior perforation in the capsule to the vicinity of the operculum at the apex of the acrosome (Fig. 2B). The perforatorium in *Trapezia* is a stout cylinder, slightly tapering anteriad, with a bluntly pointed tip and a posterior stalk constricted at the thickened ring. This form, together with differentiation of the perforatorium into a central dense fibrous core, is indistinguishable from that stated to be distinctive of xanthids (see *Pilodius*, Fig. 3) by Jamieson (1989a). In cross section, the perforatorium is seen to contain, as in xanthids and portunids (Jamieson, 1991) many circular profiles resembling microtubules though differing from typical microtubules in varying in size and in sometimes being irregular in section (Fig. 2D).

Cytoplasm

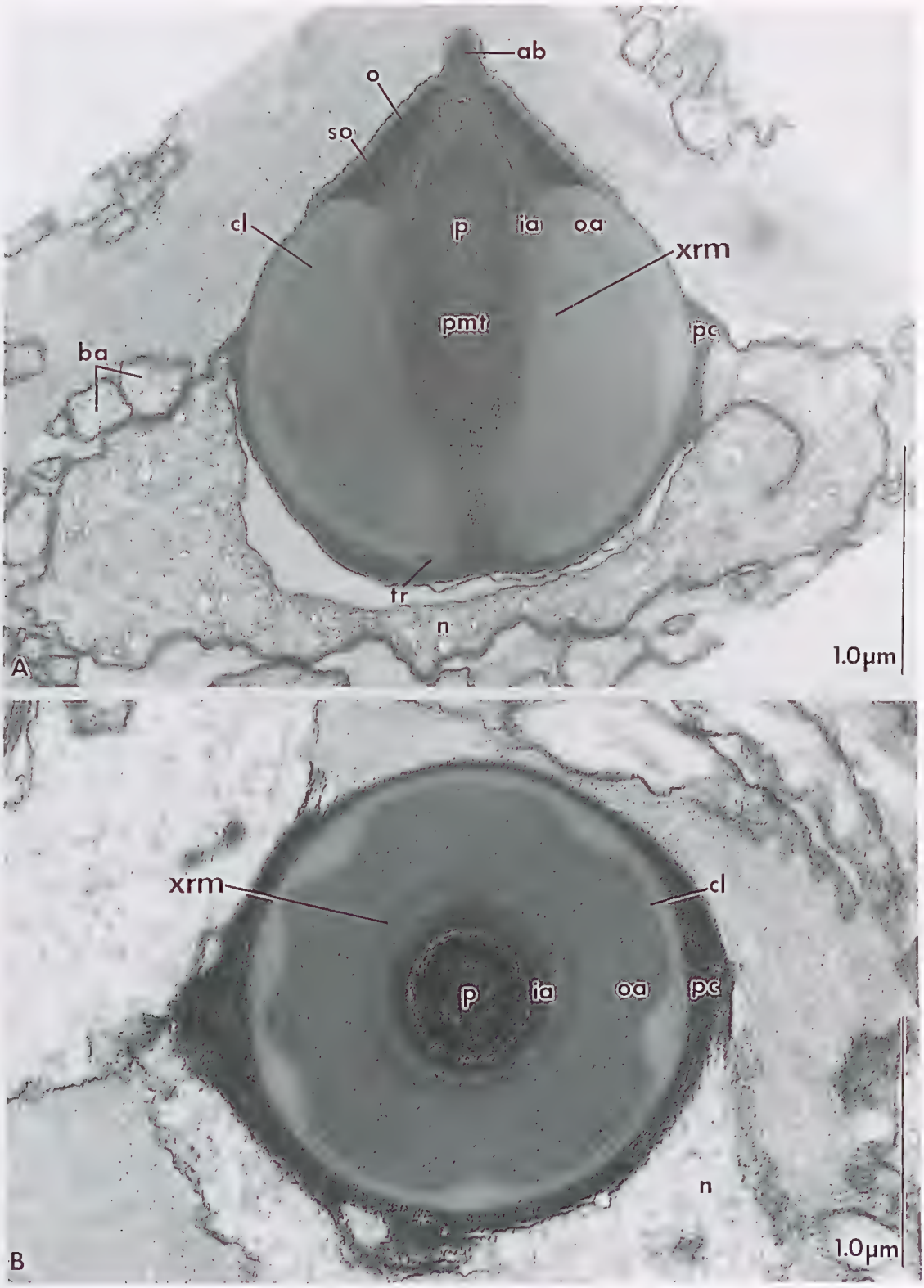
A thin layer of spermatozoal cytoplasm surrounds the acrosomal capsule. As in portunids, dorippids and xanthids the cytoplasm does not extend into the arms. In majids, in contrast, the cytoplasm extends into the lateral arms together with contained microtubules which are not discernible in the other heterotremes mentioned. In *Trapezia* the cytoplasm is enlarged anterolaterally on one side of the capsule and contains several subspheroidal and apparently degenerating mitochondria with sparse cristae (Figs 2D,E). The degree of representation of mitochondria is variable in other heterotremes, usually being negligible, though it is similar to that in *Trapezia* in the thoracotreme *Macrophthalmus crassipes* and the archaeobrachyuran *Ranina ranina* (see Jamieson, 1991). The postacrosomal cytoplasm, typical of brachyurans and well developed in *Trapezia*, contains two centrioles (Figs 2B,C), a plesiomorphic condition seen in majids, parthenopids, calappids, portunids, dorippids and *Macrophthalmus* but absent in xanthids (Fig. 3) and, usually, in thoracotremes (see Jamieson, 1991).

Contorted membranes are present among the mitochondria of the dilated region of the cytoplasm and in extensions of the cytoplasm into the chromatin (Fig. 1, 2B). These membranes are the equivalent of the sometimes better developed lamellar structure seen in other brachyuran sperm. In *Trapezia* some of the membranes are continuous with the multilaminar prenuclear membrane (see below) and also appear to be continuous with membranes of disintegrating mitochondria. It seems possible, therefore, that the multilaminar membrane is at least partly derived from mitochondrial membranes.

Nucleus

In *Trapezia*, as in xanthids, and other brachyurans, the nuclear material is located in the lateral arms and their branches (Fig. 2B) and in the cup-shaped structure around both the acrosome and its cytoplasmic sheath. The chromatin extends around the operculum, leaving only the raised central area of this exposed (Fig. 2B), as in xanthids, whereas in portunids and *Neodorippe* the operculum is not covered. The envelope between the chromatin and the basal cytoplasm is unusually well developed in *Trapezia* and is represented by a dense double membrane bounding the cytoplasm (the nature of which is obscure as it cannot be the plasma membrane). Posterior to this membrane, bounding the anterior face of the nucleus, a series of six or more dense membranes (inner nuclear membrane in Fig. 2B), make up a multilaminar membrane. In xanthids and *Portunus*, for instance, the nuclear envelope though retained is disrupted and is not multilaminar. Nevertheless, the multilaminar membrane in *Trapezia* is incomplete, as it ends anteriorly at the lamellar structures. The external, basal surface of the cell, is bounded by a dense membrane, which may represent fused nuclear and plasma membranes, here termed the cell membrane (Fig. 2B). The general chromatin consists of electron dense filaments in a pale matrix, as in most brachyurans, but is less densely packed than in xanthids (see Discussion).

FIG. 4. *Mictyris longicarpus*, a mictyrid thoracotreme. A. Transmission electron micrograph of a longitudinal sagittal section of the spermatozoon. B. Transverse section to show the 'onion ring' lamellation of the acrosome. Abbreviations: ab = apical button of operculum; ba = branches of lateral arms; cl = concentric 'onion ring' lamellation; ia = inner acrosomal zone; n = nucleus; o = operculum; oa = outer acrosomal zone; p = perforatorium; pc = vestigial periacrosomal cytoplasm; pmt = microtubules of perforatorium; so = subopercular zone; tr = thickened ring; xrm = putative modification of xanthid ring.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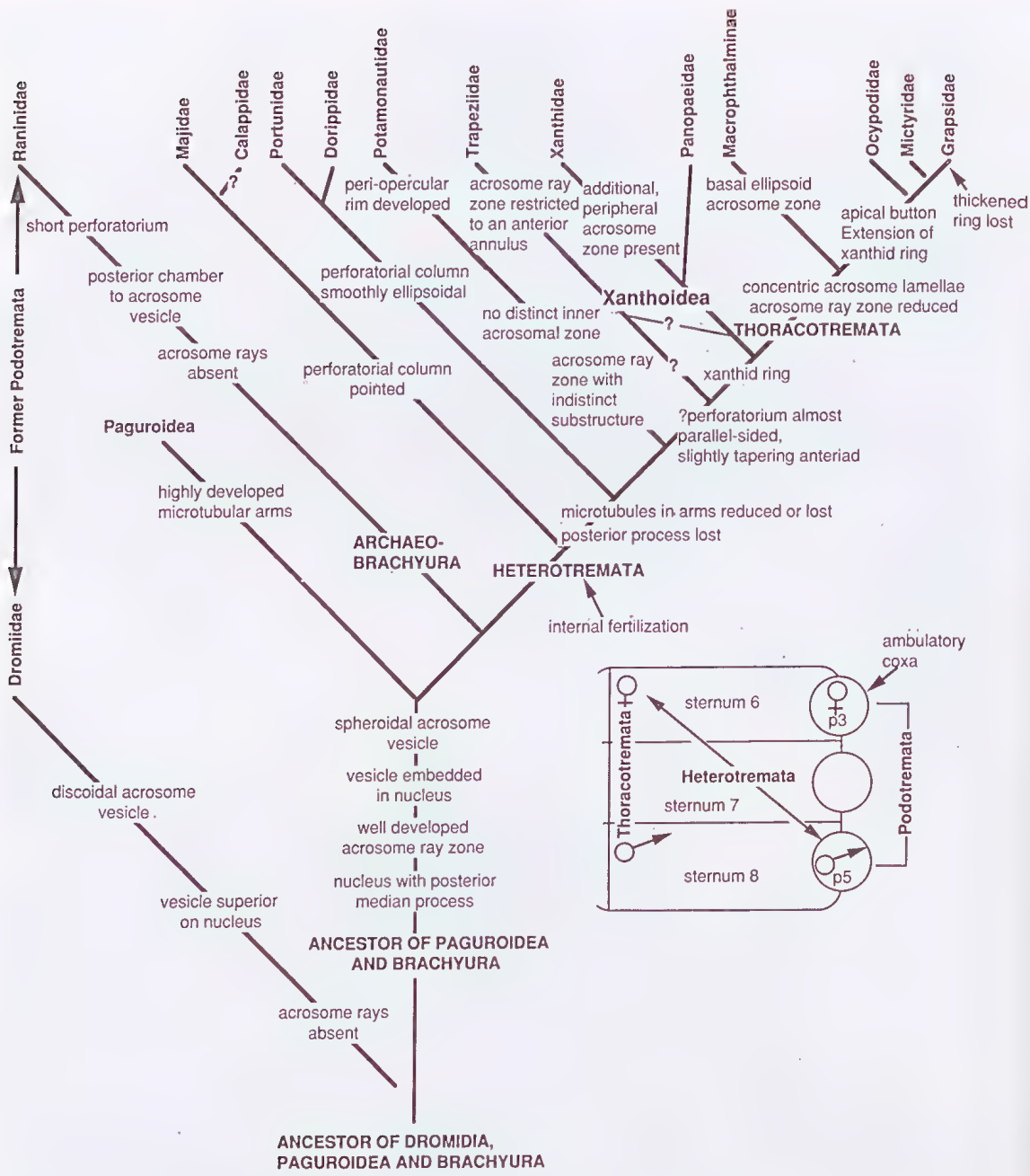

FIG. 5. Tentative phylogeny of the Brachyura based on apparent trends in the evolution of spermatozoal ultrastructure (modified from Jamieson, 1991). The chart of taxonomic features of location of gonopores is after Guinot (1978). The basal position of the Dromiidae, below the Paguroidea, which was tentatively suggested as an alternative to a brachyuran relationship by Jamieson (1991), is supported by evidence from rRNA (Spears et al., in preparation, cited in Abele, 1991). The position of the Potamonautidae is based on description of the sperm of *Potamonautes* by Jamieson (1993).

DISCUSSION

We may now consider the relationships of *Trapezia* as indicated by spermatozoal ultrastructure. These are tentatively indicated in Figure 5 within the context of a phylogeny of the Brachyura based on apparent trends in spermatozoal evolution

The following are features of the spermatozoon of *Trapezia* that are general for heterotremes: extension of the subacrosomal chamber almost to anterior apex of the sperm whereas it reaches only to the approximate equator of the acrosome in the archaeobrachyuran *Ranina*; division of the acrosome contents into inner and outer zones; presence of an acrosomal ray zone at the periphery of the inner acrosomal zone; presence of a thickened ring where the capsule surrounds the base of the subacrosomal chamber; and absence of thoracotreme features mentioned below. A feature shared with 'higher' heterotremes is the restriction of cytoplasm to the periacrosomal region; unlike majids, for instance, it does not extend into the arms. The sperm of *Trapezia* thus confirms its heterotreme status and endorses separation from thoracotremes (Guinot, 1977, 1978) on the basis of the arrangement of the genital pores.

Features of the spermatozoon of *Trapezia* that are shared with the Xanthidae (compare Figs 2B & 3), at least as exemplified by investigated Xanthinae and Chlorodiinae , and the Panopeidae, exemplified by *Eurytium limosum*, include all of the above general heterotreme features but also the following apparently apomorphic xanthid features: the structure of the perforatorium, tapering anteriad, with a fibrous core; and extension of the chromatin around the operculum, leaving only the raised central area of this exposed, the latter feature less developed in *Eurytium* than in the xanthids. These features are of questionable significance and could possibly arise homoplasically. Nevertheless, the form of the perforatorium is shared only with xanthids and *Eurytium* and, bearing in mind differences in sperm structure from the latter family outlined below, is not inconsistent with recognising relationship of *Trapezia* with xanthids though in a separate family.

Peculiar features of xanthids (Xanthinae, Chlorodiinae) (Jamieson, 1989a, and this study) and panopaeids (Jamieson & Abele, unpublished) which separate them from all other investigated heterotremes are the dense 'xanthid ring' around the base of the subacrosomal chamber and, in xanthids only, the additional peripheral zone outside the outer acrosomal zone (Fig. 3). A presumed derivative of the xanthid ring occurs in thoracotremes (see *Mictyris*, Fig. 4A) and this fact suggests that the Xanthidae are an advanced heterotreme group near the base of the Thoracotremata (see Jamieson, 1991). Presence of the ring or its derivatives indicates that although the xanthids and such thoracotremes form a monophyletic group, the Xanthoidea, as it is currently understood, is a paraphyletic group. The absence of the ring in *Trapezia* may parsimoniously be taken to be plesiomorphic rather than due to loss because loss would involve one extra evolutionary step. This, with the xanthid-like perforatorium and undoubted somatic similarities of *Trapezia* and xanthids, suggests that *Trapezia* is the plesiomorphic sister- taxon or, at least a neighbouring taxon, of the xanthid-panopaeid assemblage in so far as they are represented spermatologically by xanthines, chlorodiines and panopaeids. In *Geryon* the ring is also absent (Jamieson, 1991, from micrographs by Hinsch, 1988). The condition in other xanthoids is unknown.

Whereas the sperm of *Trapezia* shows clear heterotreme features, it lacks thoracotreme features, well exemplified by *Mictyris* (Fig. 4A,B), which include the perforate operculum with apical button (excepting *Macrophthalmus*); absence of the acrosome ray zone; absence of the thickened ring; and presence of concentric 'onion ring' lamellation of the outer acrosome zone (excepting *Uca*).

In conclusion, spermatologically *Trapezia* confirms its heterotreme position, shows features (especially the form of the perforatorium) linking it with xanthids and panopaeids, but warrants separate familial status in lacking the xanthid ring. It remains to be seen whether examination of sperm ultrastructure in further xanthoids will confirm this conclusion.

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I am deeply grateful to Dr Danièle Guinot for providing information on the taxonomic status of *Trapezia*. I am also indebted to Miss Jenny Munoz for making some observations, Mrs L. Daddow, Mr C Tudge and Mr D. Scheltinga for technical assistance, to Mr P. Davie and Mr J. Short for identifying *Trapezia coerulea*, and to to Mr C. Tudge and an anonymous reviewer for constructive comments on the manuscript. The computer-generated line drawings are by the

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A TAXONOMIC REVISION OF THE EASTERN AUSTRALIAN EARTHWORM GENUS *PERISSOGASTER* FLETCHER (MEGASCOLECIDAE: OLIGOCHAETA)

B.G.M. JAMIESON

Jamieson, B.G.M. 1993 06 30: A taxonomic revision of the eastern Australian earthworm genus *Perissogaster* Fletcher (Megascolecidae: Oligochaeta). *Memoirs of the Queensland Museum* 33(1): 235-244. Brisbane. ISSN 0079-8835.

The three species assigned to *Perissogaster* by Fletcher are redescribed. Of these *P. nemoralis* and *P. queenslandica* are shown to have on each side in caudal segments a median nephridium with preseptal funnel flanked by astomate meronephridia, all nephridia being exonephric. This dichogastrin condition of the nephridia, coupled with multiplication of gizzards, is considered to warrant placing the two species in the genus *Digaster* Perrier. The trigastric condition is verified for *P. nemoralis* but *P. queenslandica* is shown to have only two gizzards. It is demonstrated for the first time that *P. excavata*, the trigastric type species of *Perissogaster*, has at least 100, mostly preseptal, nephrostomes on each side per segment caudally, a condition attributable to the Tribe Megascolecini. It is nevertheless argued that this species is closely related to *Digaster*. Parsimony analysis is equivocal between origin of *P. excavata* within *Digaster* or a sister-group relationship to the *Digaster-Didymogaster* assemblage. The latter derivation is compatible with (though not necessitating) parallel development in *P. excavata* of multiple gizzards from a monogastric ancestor with or without multiple nephrostomes. A monotypic genus *Perissogaster* is redefined for *P. excavata*.
☐ *Perissogaster, Digaster, Didymogaster, nephridia, taxonomy, parsimony analysis.*

B.G.M. Jamieson, Department of Zoology, University of Queensland, Queensland 4072, Australia; 15 March, 1993.

Perissogaster was erected by Fletcher (1887) for a new species, *P. excavata*, which differed from all known Australian oligochaetes in possessing three gizzards. Subsequently, Fletcher 1889, included *P. nemoralis* and *P. queenslandica* on the grounds that they also were trigastric.

Beddard (1895) placed *Perissogaster* and *Didymogaster* in *Digaster* because the three entities shared lobate prostates, meronephridia and more than one gizzard and were restricted to Australia. Michaelsen (1900) again separated the three genera but Sweet (1900) and Jamieson (1963) included the three species of *Perissogaster* in *Digaster* while excluding *Didymogaster*. Jamieson (1970, 1971) showed that *P. queenslandica* had dichogastrin nephridia (a stomate exonephric meronephridium median to astomate meronephridia on each side in caudal segments) and could therefore be retained in *Digaster* which has the same nephridial condition. It was, however, suggested that *P. excavata* and *P. nemoralis* should be excluded from *Digaster* in a reinstated *Perissogaster* as only astomate nephridia were demonstrated. *Perissogaster* was formally restricted to these two species by Jamieson (1975) but it was stated that the existing material of the genus was not in sufficiently good condition to allow full characterisation of the genus. The kindness of Dr Courtenay Smithers in forwarding to the author a well preserved specimen which has proved to be *Perissogaster excavata* has allowed a reappraisal of the anatomy of this species revealing an unsuspected nephridial anatomy and has prompted redescription of the types of *P. nemoralis* and *P. queenslandica* which, again, are found to differ significantly from previous descriptions.

All figures are drawn by camera lucida. The following abbreviations are used in Figs 1&2: ♀, female pore; g.m. accessory genital marking; ♂ male pore; ♀ po, male porophore; pr.d, prostate duct; pr.g. glandular portion of prostate; sp. amp, spermathecal ampulla. sp. div, spermathecal diverticulum; sp.p, spermathecal pore; v.d, vas deferens. Roman numerals indicate respective segments. Registration numbers prefixed by AMW are housed in the Australian Museum.

TAXONOMY

Perissogaster Fletcher, 1887 emend.

Type species: *Perissogaster excavata* Fletcher, 1887.

DIAGNOSIS

Setae lumbricine. Gizzards 3, in V, VI and VII; extramural calciferous glands absent. Mero-

nephric; with numerous preseptal funnels on each side in each intestinal segment. Combined pores of a pair of tubuloracemose prostates and the vasa deferentia in XVIII. Spermathecae with pores at the anterior margins of their segments.

Detailed Definition

Setae 8 per segment; dorsal setal couple (*cd*) significantly wider than the ventral couple (*ab*). Clitellum anterior to the male pores. Combined male and prostatic pores a pair on XVIII. Accessory genital markings present. Female pores a minute pair presetally in XIV. Spermathecal pores 2 pairs, in 7/8 and 8/9.

Some preclitellar septa very strongly thickened. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XII, those in X-XII latero-oesophageal; preceding commissurals dorsoventral only; supra-oesophageal vessel oesophageal only; a pair of anterior lateroparietal trunks becoming latero-oesophageal and passing median to the dorsoventral commissurals to join the oesophageal plexus. Subneural vessel absent. Three oesophageal gizzards in V, VI and VII; extramural calciferous glands absent; intestine commencing in XVI, lacking muscular thickening, caeca and typhlosole.

Meronephric; enteronephric tufts in II-IV; astomate exonephric parietal micromeronephridia in succeeding segments but from XIV to the caudal extremity numerous preseptal nephrostomal funnels on each side in each segment; intestinal enteronephry not demonstrated. Holandric; gymnorchous; seminal vesicles in IX and XII. Prostates 1 pair, tubuloracemose. Fan shaped ovaries, and funnels, in XIII. Spermathecae short-stalked with small, sessile, lobed diverticulum.

Distribution

New South Wales: Hawkesbury to Hunter River districts.

Remarks

The presence of multiple nephrostomes here demonstrated for *P. excavata* for the first time, sets *Perissogaster* apart from *Digaster*, no other described characters necessitate separation of the two genera.

Perissogaster excavata Fletcher, 1887
(Figs 1A, 2A, B)

Perissogaster excavata Fletcher, 1887: 383-387.
Digaster excavata; Beddard, 1895: 486; Sweet, 1900: 123. Buchanan, 1909: 73; Jamieson, 1963: 85-90; 1971: 75.
Perissogaster excavata; Fletcher 1889: 1528; Michaelsen, 1900: 193; 1907: 162; Bage, 1910: 231; Jamieson, 1970: 44; 1975: 268-269.

Material Examined

'Tuglo' property, near Mt Royal, 48km north of Singleton, under a stone on very clayey muddy soil, collector C.N. Smithers, 8 February, 1976 – 1 clitellate specimen, AMW6644. Identification checked against a badly macerated much-dissected type specimen from Morpeth, AMW 1457.

Description

Length = 280mm, width (midclitellum) = 16mm, greatest width (forebody) = 18mm, 175 segments (69-334mm long, 3-15mm wide, 160-195 segments; Fletcher, 1887). Form circular in cross section. Segments II and III biannulate ; remaining segments to XIV triannulate, IV weakly, the others strongly; thereafter with a strong postsetal furrow. Pigmented grey, excepting the pale ventrum, in alcohol. Prostomium proepilobous, short and broad, it and the peristomium with many longitudinal furrows. Dorsal pores absent (sometimes about 20 rudimentary pores posteriorly, Fletcher, 1889: 1528). Setae in 8 regular longitudinal rows throughout, commencing on II; minute but distinctly visible; setae *a* and *b* not visible in XVIII. In XII *aa*:*ab*:*bc*:*cd*:*dd* = 2.96:1.00:1.60: 1.50:2.68; circumference = 55mm; *dd*:*u* = 0.19. Nephropores not externally recognisable. Clitellum annular, XIV-XVII, with weak development to 1/2XIII and 1/2XVIII dorsally; (1/3XIII-part or most XVIII; Fletcher, 1887) intersegmental furrows and setae retained. Male pores (Fig. 1A) , from internal examination, on small indistinct elliptical papillae equatorially in XVIII in *ab* (not visible externally; Fletcher, 1887). Accessory genital markings paired presetal eye-like markings in XVIII-XXII in *bc* and a transverse glandular trough similarly located in XXIII but continuous across the ventrum; the markings in XVIII also lying in a transverse elliptical trough which impinges on the posterior region of XVII; the troughs in XVIII and XXIII with numerous longitudinal stigmata; the accessory markings and male pores lying in a rectangular flattened and thickened area. (Accessory markings limited to XVIII-XXI; Fletcher, 1887). Female pores small but distinctly visible, a pair presetally and well median of *a* lines of XIV in a common whitish glandular area which interrupts the clitellum pre-

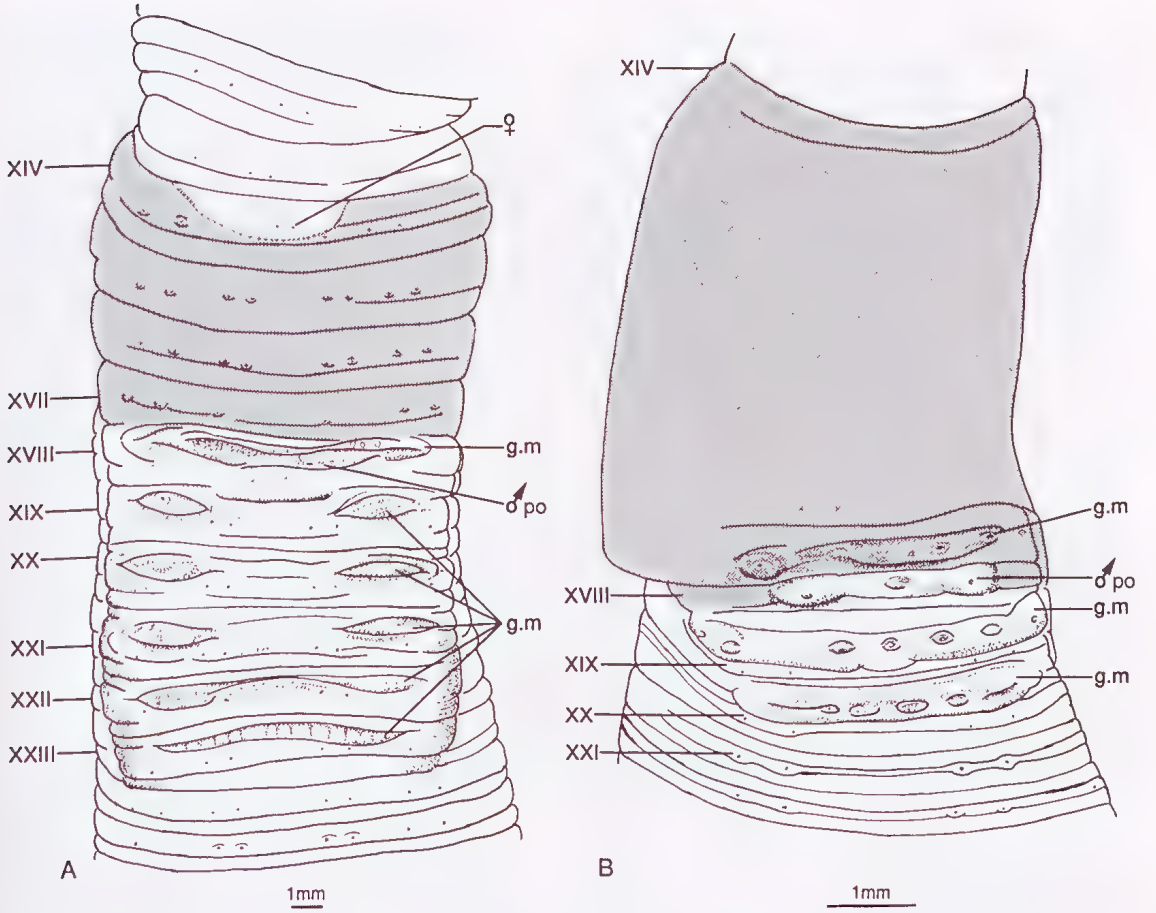
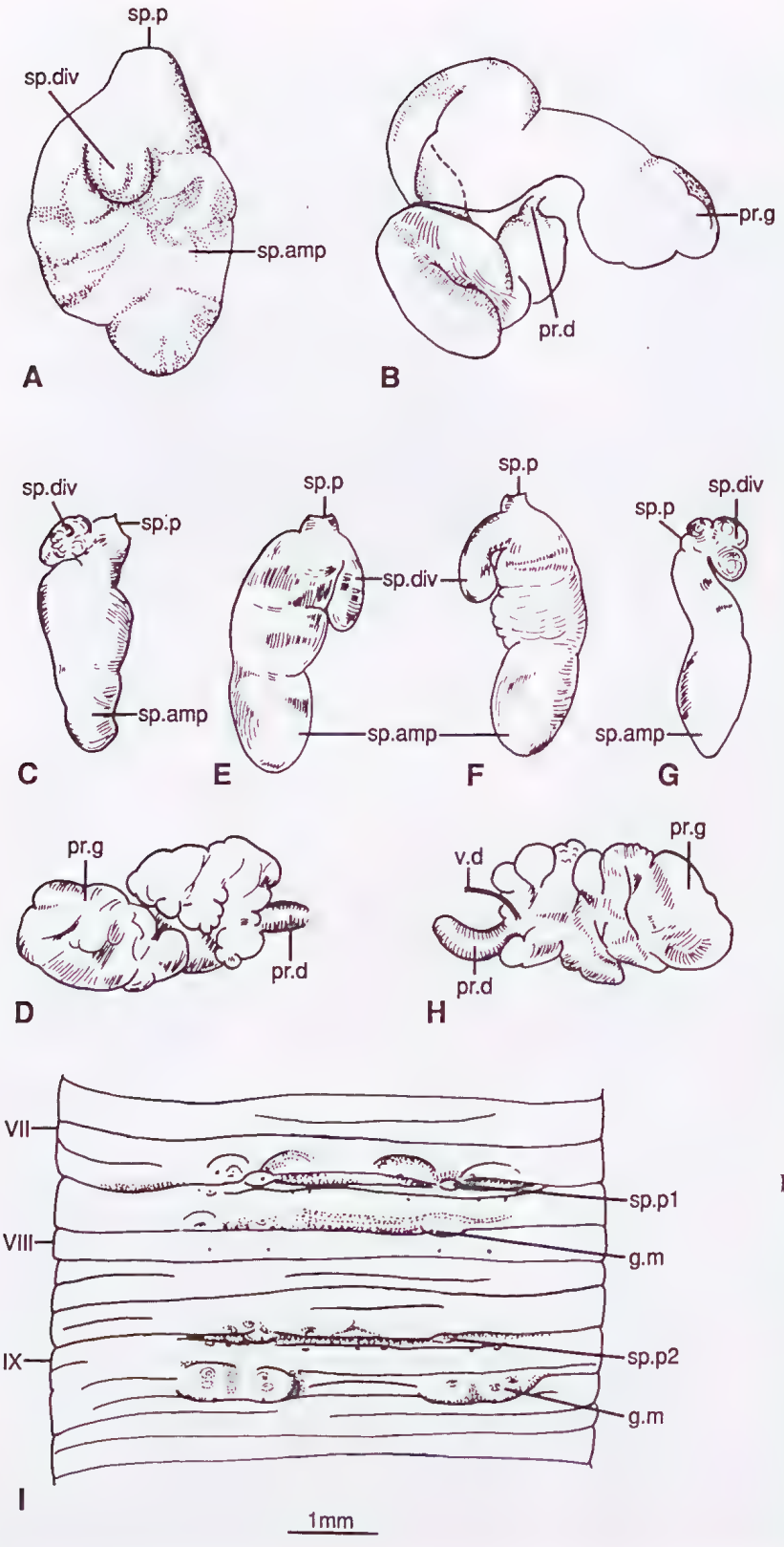


FIG. 1. Genital fields. A, *Perissogaster excavata* (TUGLO specimen); B, *Digaster nemoralis* (paralectotype). Clitellum shaded.

setally. Spermathecal pores not externally visible, in 7/8 and 8/9, appearing from internal examination to lie in *b* lines but stated by Fletcher (1887) to be in *a* lines.

Some preclitellar septa thickened; 9/10-12/13 (-13/14; Fletcher, 1887) immensely strong; tendons connecting the septa, of which those between septum 5/6 anteriorly are very strong. Dorsal blood vessel single, continuous onto the pharynx and passing under the brain. Last hearts in XII, those in X-XII large and latero-oesophageal, each receiving a broad short connective from the supra-oesophageal vessel and a longer slender connective from the dorsal vessel but otherwise unbranched; commissurals in V-IX (IV- IX; Buchanan, 1909) slender and dorsoventral only, though valvular, and each giving a lateral branch to the body wall before joining the ventral vessel. Supra-oesophageal from 3/4IX to XIII (VIII-XIII; Buchanan, 1909), rudimentary in the last segment; adherent to the oesophagus. A large, free latero-oesophageal trunk present on each side, median to the dorsoventral commissurals in V-IX, ending in the plexus on the floor of the oesophagus in IX and continuous in IV anteriorly as a thick longitudinal ventrolateral parietal trunk. Subneural vessel absent. Oesophagus forming 3 large subspherical strongly muscular gizzards, in V, VI and VII, decreasing in size posteriad, each constricted off from but abutting on the others without appreciable intervention of unmodified oesophagus (connected by short pieces of oesophagus; Fletcher, 1887). The oesophagus simple, lacking calciferous glands, in VIII-XV, though internally with low papillae. Intestine commencing in XVI, muscular thickening, caeca and typhlosole absent. Nephridia meronephridia: tufts of numerous astomate micromeronephridia



on and lateral to the pharynx in II, III and IV send composite ducts to the pharynx in III and IV and those of II to the buccal cavity; numerous minute astomate exonephric parietal micromeronephridia in V-XIII, becoming very dense in XIV in which many are, in addition, adherent to the posterior septum; very numerous shortly stalked nephrostomes present on the anterior face of septum 14/15 and apparently arising mostly from the dense bands of exonephric septal nephridia on the posterior face of this septum. Nephridia in XV and succeeding segments dense bands on the anterior and posterior septa, with numerous funnels restricted to the anterior face of the posterior septum; parietal nephridia few but at least some of them with funnels. By XIX the nephridial bodies are chiefly on the posterior face of each septum, with more than 100 stalked funnels on the anterior face of the septum on each side; parietal nephridia are very few. In the caudal region nephridia are dense on the anterior faces of the septa, co-

FIG. 2. A,B, *Perissogaster excavata* (paralectotype): A, left spermatheca of IX; B, right prostate. C, D, *Digaster queenslandica* (lectotype): C, left spermatheca of IX; D, left prostate. E-I, *Digaster nemoralis*: E,F, ventral and dorsal views of left spermatheca of IX (lectotype); G, right spermatheca of IX (paralectotype); H, right prostate (paralectotype); I, spermathecal genital field (paralectotype).

existing with numerous stalked funnels and less numerous, with very few evident funnels, on the posterior faces, parietal nephridia are absent; no enteronephry is demonstrable.

Testes and large iridescent funnels in X and XI; testis-sacs absent; seminal vesicles racemose, much divided, in IX and XII, the posterior pair the larger. Prostates (Fig. 2B) tubuloracemose, restricted to an enlarged segment XVIII (or unilaterally in XVIII and XIX; Fletcher, 1887) each basically a broad tortuous tube but with some portions, particularly at the ental end, fused so that the tubular form has in places been lost; almost sessile, the short duct being concealed in the body wall (vas deferens opening into the duct at the base of the gland; Sweet, 1900). Fan-shaped ovaries, and funnels, in XIII. Spermathecae (Fig. 2A) 2 pairs, in VIII and IX, each virtually sessile on the body wall, with flattened ovoid ampulla and short broad diverticulum on its anterodorsal surface, the diverticulum more or less bi- or trilobed.

Digaster Perrier, 1872

D. nemoralis must now be added to the genus, as redefined by Jamieson (1975), as it is here shown to have the dichogastrin condition of the nephridia seen in all species of *Digaster*. The following changes in the definition are necessitated by the present study: *P. queenslandica* must be excluded from the statement that there may be 3 gizzards (see account below). This number is now limited in *Digaster* to *D. nemoralis* and variant individuals (Jamieson, 1963) of *D. perrieri*. The intestinal origin in the genus is now XVI-XIX and absence of a typhlosole is no longer constant as a typhlosole is present in *D. nemoralis*.

Digaster nemoralis (Fletcher, 1889) (Figs 1B, 2E-I)

Perissogaster nemoralis Fletcher, 1889: 1527-1528.
Digaster nemoralis; Beddard, 1895: 486; Jamieson, 1963: 86; 1971: 75.
Perissogaster nemoralis; Michaelsen, 1900: 198; Jamieson, 1970: 44; 1975: 268-269.

Material Examined

Gosford, New South Wales, 2 clitellate, much dissected type specimens, AMW1438, here designated the lectotype (L) and paralectotype (P).

Description

Length = 90+, 105mm, width (midclitellum) = 5.5mm, greatest width (forebody) = 6mm (lectotype, paralectotype), segments (P) 192. Form circular in cross section. Segments I-III simple; IV biannulate with the setae on the anterior annulus; from V, segments quadriannulate with the setae on the second annulus, and often with faint additional furrows; postclitellar segments triannulate. Pigmentless buff in alcohol. Prostomium broad, prolobous or perhaps slightly proepilobous, it and the peristomium with many longitudinal furrows. Dorsal pores visible posteriorly, location anteriorly indeterminable owing to previous dissection (commencing after about X; Fletcher, 1889). Setae minute, in 8 regular longitudinal rows throughout, commencing on II; setae *a* and *b* replaced by penial setae in XVIII; in XII *aa*:*ab*:*bc*:*cd*:*dd* = 3.25:1.00:3.30:1.94:13.09; circumference = 15.4mm; *dd*:*u* = 0.47. Nephropores not externally recognisable. Clitellum annular, XIV-1/2XVIII; intersegmental furrows, dorsal pores and setae suppressed. Male pores in XVIII (Fig. 1B) on distinct ellipsoidal papillae, in *a* lines; the two papillae medianly conjoined by a transverse boss which widens medianly around a midventral oval pit-like glandular stigma. A median transverse pad present in each of intersegments 17/18, 18/19 and 19/20, each with a transverse series of similar stigmata. Numerous stigmata associated with tumescence (Fig. 2I) also present in VII, VIII and IX in association with the spermathecal pores. Female pores not visible. Spermathecal pores on distinct papillae in 7/8 and 8/9, in *a* lines.

Some preclitellar septa thickened: 5/6-9/10 very strong. Dorsal blood vessel single, anterior course indeterminable owing to previous dissection. Last hearts in XIII; those in X-XIII large and latero-oesophageal, each receiving a broad short connective from the supraoesophageal vessel and a longer slender connective from the dorsal vessel but otherwise unbranched; commissurals in VIII (and IX?; and further anteriorly?) slender and dorsoventral only and each giving a lateral branch to the body wall before joining the ventral vessel. Supraoesophageal vessel narrow and adherent to the oesophagus but limits indeterminable. Broken latero-oesophageal trunks observed in segment VI. Subneural vessel absent. Oesophagus forming 3 large strongly muscular gizzards, in V, VI and VII, each bowl-shaped and occupying the posterior half of the segment, the oesophagus in the anterior half being similarly dilated but only slightly muscularised. Oesophagus very short,

almost suppressed, in VIII; in IX and X short but laterally expanded and in XI-XIV forming paired,very conspicuous, strongly vascularised dilatations, increasing in size posteriorly to very large in XIV; these dilatations dorsolateral, internally with numerous low lamellae but not constricted off from the general oesophageal lumen. Oesophagus in XV and XVI narrow but invaginated into the dilatation in XIV in which it has the appearance of a rosette-like valve. Intestine commencing, with abrupt widening, in XVI; muscular thickening and caeca absent; a deep laminar dorsal typhlosole present. Nephridia meronephridia; large astomate tufts with many spiral loops in II-IV send a common (multiple?) duct forward on each side, traced anteriorly in II but further course indeterminable. Smaller aggregates with lateral outliers in V to VII are restricted to the posterior septum but are exonephric by separate individual ducts, one from each nephidium. By VIII the nephridia form a transverse exonephric band of several moderately large meronephridia at junction of posterior septum and body wall. By XII the band of several nephridia on each side is parietal with the forwardly directed ducts entering the body wall presetally; from XIII there is an increasing tendency for the median nephridia to form diffuse aggregations, though by about XXII these aggregations have reduced to 2 to 3 nephridia lateral to which are 4 smaller nephridia forming regular longitudinal rows; all nephridia are exonephric, avesiculate and apparently astomate. Towards the caudal end there are 3 well spaced nephridia on each side in very straight longitudinal rows lateral to what appear to be two or more aggregated nephridia. In the paralectotype which, unlike the lectotype, is complete posteriorly, the median-most nephridium in several posterior segments has a preseptal funnel and is enlarged as an exonephric megameronephridium. Finally in approximately 7 most posterior segments the regular arrangement of nephridia breaks down, nephridial loops filling the segments transversely and the median nephridium is further enlarged; the lateral nephridia appear to be interconnected by a medianly directed duct; the median nephridium retains the preseptal funnel but whether it and the lateral nephridia are exonephric or enteronephric is indeterminable. Testes and large iridescent sperm funnels in X and XI; testis-sacs absent; seminal vesicles racemose, large, in IX, XI and XII. Prostates (Fig. 2H) racemose: subrectangular deeply incised lobes, with stout moderately long muscular duct which branches within the gland and entally receives the vas deferens. Penial setae slender entally strongly curved needles, the ectal tip delicately pointed with recurved extremity; ectal region with a few fine apically directed spines; a mature seta (paralectotype) 0.96mm long; the shaft 21 µm wide at midlength. Bushy ovaries and funnels, in XIII; ovisacs not recognisable. Spermathecae (Fig. 2E,F,G) 2 pairs, in VIII and IX, each with elongate sacciform to pointed ovoid ampulla which is joined ectally and anteriolaterally by a clavate inseminated diverticulum, duct ectal to the ampulla very short. In the paralectotype the diverticulum is bi- or usually multi-loculate.

Digaster queenslandica (Fletcher, 1889) (Fig. 2C,D)

Perissogaster queenslandica Fletcher, 1889: 1529-1530.

Digaster queenslandica; Beddard, 1895: 485; Sweet, 1900: 124; Jamieson, 1970: 44; 1971: 75; 1975: 268-269.

Perissogaster queenslandica; Michaelsen, 1900: 199; 1916: 22-24.

Material Examined

Oxley, southeast Queensland, collector T.G. Sloane, AMW1408, two specimens here designated lectotype (L) and paralectotype (P).

Description

Length = 162mm, width at segment XV = 6.5mm, greatest width (forebody) = 8mm, segments 215. Form circular in cross section but with some ventral flattening posteriorly. Segments I to III simple; from IV biannulate with setae on the posterior annulus and sometimes with weaker further annulation; simple from approximately XX posteriorly. Pigmentless buff in alcohol. Prostomium prolobous though longitudinal furrowing of the peristomium perhaps includes a narrow dorsal tongue. Dorsal pores unusually obvious, first in 4/5 but with a rudiment in 3/4. Setae in 8 regular longitudinal rows throughout, *a* and *b* absent in XVIII; in XII, *aa*:*ab*:*bc*:*cd*:*dd* = 2.57:1.00:2.00:1.78:18.57; circumference = 21.5mm; *dd*: $u = 0.60$. Nephropores not externally recognisable. Clitellum not developed. Male pores in XVIII, in *a* lines, on small almost contiguous papillae. Female pore unpaired in XIV, midway between the setal arc and anterior margin. Spermathecal pores 2 pairs, minute but distinctly visible in VIII and IX, appreciably be-

hind the anterior margin; those in IX 0.55mm apart.

Septa 4/5 and 5/6 fairly strongly thickened; 6/7 and 7/8 slightly thickened; 8/9 moderately strongly; 9/10-13/14 strongly thickened, 11/12-13/14 especially so. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XII; those in X-XII large and latero-oesophageal, each receiving a broad short connective from the supra-oesophageal vessel and a slender connective from the dorsal vessel but otherwise unbranched; commissurals in (V?) VI-IX slender and dorsoventral only and each giving a lateral branch to the body wall before joining the ventral vessel. Supra-oesophageal vessel well developed in X-XII, weakly developed in IX and 1/2XIII. A large latero-oesophageal trunk on each side median to the commissurals joining the supra- oesophageal vessel in X and traceable forward at least to VI. Subneural blood vessel absent. Oesophagus with only 2 gizzards (contrary to Fletcher, 1889), in VI and VII, each very large, strongly muscular and subcylindrical, abutting on each other with almost inappreciable intervening oesophagus; that in VI preceded in the anterior portion of the segment by unthickenened oesophagus. The oesophagus in V dilated to almost the size of a gizzard but its musculature unthickened, a spurious impression of a gizzard being produced by the ensheathing muscular septum 5/6. Dilatation and vascularisation of the oesophagus in XIV-XVI but no calciferous glands. Intestine cornmencing in XVIII; muscular thickening absent; caeca and typhlosole not recognisable but maceration precludes certainty. Nephridia all avesiculate meronephridia: dense aggregations of meronephridial tubules on the parietes in II-IV appear exonephric but tubules adherent to the pharynx are possibly enteronephric; from V to the anterior intestinal region astomate, avesiculate micromeronephridia scattered on the parietes, the nephridia decreasing in size and becoming more numerous (many) posteriorly; never forming regular longitudinal rows. Caudally, in the last approximately 18 segments, with 15-20 astomate parietal micromeronephridia in transverse single file on each side lateral to an exonephric(?) megameronephridium with large preseptal funnel. Testes and funnels in X and XI, funnels in XI larger and iridescent; seminal vesicles large, racemose, in XI and XII. Prostates (Fig. 2D) depressed elongate tongue-shaped, sufficiently incised to be considered racemose but with a main, central canal from which many lesser side branches supply the lobes; ectal duct short, weakly muscular and largely concealed in loose parietal musculature. Penial setae absent. Ovaries presumably represented by a pair of large depressed lobes with no evident oocytes on the anterior septum of XIII; funnels on the posterior septum. Spermathecae (Fig. 2C) 2 pairs, in VIII-IX, each with conical-ovoid ampulla and short, wide duct: which is joined anterolaterally by a compact inseminated internally multiloculate and externally slightly lobed diverticulum.

Remarks

The demonstration above that Fletcher and Michaelsen were incorrect in recognising a third gizzard in this species gives unexpected support to the author's contention (Jamieson, 1970) that the previously described anatomy and the hitherto unrecognised dichogastrin condition of the nephridia warranted placing it in *Digaster*.

Michaelsen (1916) recorded this species from Brisbane, southeast Queensland.

CLADISTICS

As an adjunct to taxonomic considerations of the status of *Perissogaster* the relationships of the three species formerly placed in the genus to each other and to *Digaster* and *Didymogaster* have been investigated, using the PAUP program of Swofford (1990), version 3.0s, using 30 characters for 25 species (Jamieson, unpublished). Suffice to say the exhaustive and branch-and-bound search options gave a very large number of trees with grossly discordant topologies and that a consensus tree gave no resolution beyond separating the two *Didymogaster* species as the sister-group of the *Digaster-Perissogaster* assemblage. This assemblage formed a single polytomy. Many of the characters proved highly homoplasic.

A subset of 15 of the less noisy characters applied to only 11 taxa, consisting of a hypothetical ancestor (hypanc), the three *Perissogaster* species, the two *Didymogaster* species, and representatives of the *lumbricoides* and *perrieri* groups within *Digaster* (details below) produced a single tree (Fig. 3) in a branch-and-bound search. In view of the discordant results when the full character-taxon set is used, or when additional taxa are added to the reduced set, this single tree can be regarded as only one of many objective hypotheses of relationships. It is possible that the true phylogeny is not recoverable from the morphology of extant species of the total assemblage. The single tree obtained will, nevertheless be used in the following 'intuitive' discussion of

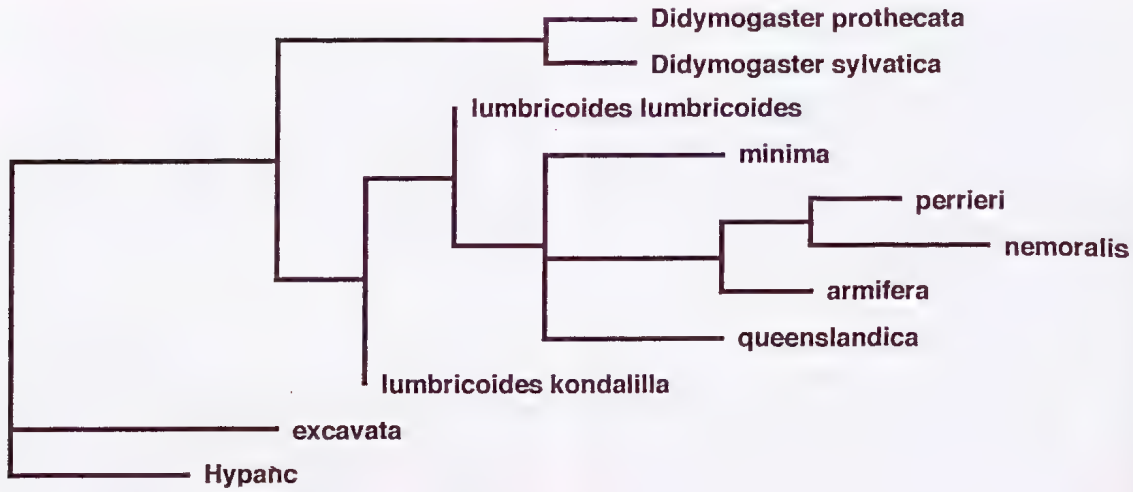


FIG. 3. Single tree obtained for 11 taxa indicated, and 15 characters, using the branch-and-bound option of the PAUP program. Tree length = 27. Consistency index (CI) = 0.778. Homoplasy index (HI) = 0.222. CI excluding uninformative characters = 0.667. HI excluding uninformative characters = 0.333. Retention index (RI) = 0.684. Rescaled consistency index (RC) = 0.532

relationships and in support of the taxonomic decision made.

An ancestor (hypanc) with a single gizzard and other characters indicated in the matrix was envisaged. Recourse, alternatively, to using the more objective out-group strategy, using *Didymogaster* as the outgroup, gave similar results.

Characters Employed

This list is a subset of those used in the more comprehensive analysis. As a result some of the characters (marked #) are uninformative or invariable. *Numbers are deducted from the states of some characters to limit their values to less than 10 and avoid hexadecimal notation.

#1. Male pore(s) unpaired 1; paired 2.
2. Female pore(s) unpaired 1, paired 2.
#3. Spermathecal pore(s) unpaired 1, paired 2.
4. First spermathecal segment.
5. Spermathecal pores, number of transverse sets.
6. Segment (-10) of last hearts.*
7. First gizzard segment.
8. Number of gizzards.
9. Caudal preseptal funnels 1, many 2.
10. Testes in X 1, X and XI 2, XI 3.
11. Seminal vesicles in IX, X, XI and XII 1, IX and XII 2, XI and XII 3, XII 4, IX, XI and XII 5.
12. Prostates tubular 1, tubuloracemose 2, racemose 3, racemose- bipartite 4.
13. Penial setae absent, 0 present 1.
#14. Number of diverticula per spermatheca.
15. Diverticula uniloculate 1, multiloculate 2.

Input Data

```
Taxon                          123456789012345
Didymogaster prothecata        222643621224011
Didymogaster sylvatica         222733621224011
Digaster lumbricoides
          lumbricoides         22282262?233011
          kondalilla           22282262?234011
       minima                  22282262?343012
       perrieri                2?282352?233111
       queenslandica           212822621232012
       nemoralis               2?2823531253112
       armifera                22282252?223112
Perissogaster excavata         222822532222011
Hypanc                         2225525112?1?11
```

Branch-and-Bound Search Settings

Initial upper bound: unknown (compute via stepwise).
Addition sequence: furthest.
Initial MAXTREES setting = 100.
Branches having maximum length zero collapsed to yield polytomies.
Topological constraints not enforced.
Trees are unrooted.
Multi-state taxa interpreted as uncertainty.
Outgroup = Hypanc.
Characters were all scored as unordered and unweighted.

DISCUSSION

From 'intuitive' taxonomic considerations, *Perissogaster nemoralis* and *P. queenslandica* are here included in *Digaster* because of the correlation of three points: general anatomy, multiplication of gizzards and dichogastrin nephridia. The dichogastrin nephridial condition occurs in earthworm genera of several zoogeographical regions of the world and has been accompanied by multiplication of the gizzard, from the usual monogastric condition, independently in the various regions. It has been argued (Jamieson, 1975) that the di- or trigastric condition in Australian earthworms originated in what is now the montane coastal province of the Eastern Sub-region, to which such forms are restricted, independently of evolution of this condition in other, non-Australian zoogeographic regions.

Multiplication of gizzards might have developed only once (strict monophyly) or in more than one lineage predisposed to this development by virtue of genetic similarity and relationship (parallelism or homoplasy). It is unlikely that a third hypothesis, development of the multigastric condition independently in unrelated taxa, is tenable as this would presuppose edaphic or other environmental factors favouring repeated development of the condition in the montane coastal province but absent from other provinces.

The taxa with multiple gizzards are (1) a large group of species, containing the type species, *D. lumbricoides* with two gizzards, in VI and VII, which is restricted to Queensland and northern New South Wales; (2) *D. perrieri* and *D. armifera*, with two gizzards, in V and VI, allopatric in New South Wales; (3) two species, comprising the genus *Didymogaster*, with the *lumbricoides* location of the gizzards, sympatric with *D. perrieri* and *D. armifera* in central New South Wales; and (4) the three species of *Perissogaster* s.lat., *P. excavata, P. nemoralis* and *P. queenslandica*.

With regard to the phylogenetic validity of these four groupings: on the basis of gizzard location the *lumbricoides* group might reasonably be assumed to form a monophyletic group. However, neither the restricted PAUP analysis (Fig. 3) nor analysis of the full taxon-character set supported monophyly.

Digaster perrieri and *Digaster armifera*, though sympatric with *Didymogaster*, differ from other *Digasters* and from *Didymogaster* in having gizzards in V and VI, and might be considered the sister-group of the *lumbricoides-Didymogaster* group. However, PAUP analyses do not support a monophyletic *perrieri-armifera* assemblage (Fig. 3).

Didymogaster has various conflicting positions in the PAUP analyses, including that of sister-group to *Digaster*, as shown in Fig. 3. Synapomorphies defining *Didymogaster* include intrasegmetal location of spermathecal pores and presence of testic-sacs (neither character used in the restricted analysis). Its generic status is accepted here.

The relationship of the three former *Perissogaster* species may now be further considered. It has been shown that *Perissogaster queenslandica* is digastric, contrary to previous descriptions, with the *lumbricoides* location of the gizzards, in VI and VII and is placeable in *Digaster*, as supported in Fig. 3 and advocated by Jamieson (1970, 1971). *P. nemoralis*, sympatric with *D. armifera* and *D. perrieri*, is here transferred to *Digaster* as its only trigastric species (excepting variant individuals of *D. perrieri*). Consideration has been given to the possibility that the *armifera-perrieri* condition (gizzards in V and VI) and *lumbricoides* condition (gizzards in VI and VII or their homeotic equivalent) have developed dichotomously from the trigastric condition seen in *nemoralis*. It has been shown above that cladistic analysis does not support recognition of either group. Conversely, the trigastric condition might be considered to reflect a further development of the propensity in *Digaster* to thicken the oesophageal musculature in two of segments V to VII. The PAUP analyses support the latter view, presenting the trigastric condition as an apomorphy of *nemoralis* developed from the digastric condition of an ancestral *Digaster* perhaps (Fig 3) shared with *D. perrieri*.

The relationships of the type species of *Perissogaster, P. excavata*, are especially uncertain. If multiple gizzards are evidence of relationship, it would appear that multiplication of nephrostomes characteristic of *P. excavata*, which would formerly have assigned it to the tribe Megascolecini sensu Jamieson (1971), has occurred in this species independently of acquisition of this condition in other genera of the tribe. This would support the author's contention that the Megascolecini may represent a grade rather than a clade. The anatomy of *P. excavata* is close to that of *P. nemoralis*, excepting the nephridial condition, extending to the origin of the intestine in XVI, unknown elsewhere in *Digaster*. However, an intuitive postulate of a sister-group relationship of *excavata* to the *Digaster-Didymogaster* assemblage is supported by the restricted PAUP

analysis (Fig. 3). It is equivocal as to whether the common ancestor of *excavata* and this assemblage had two or three gizzards despite indicating independent origin of three gizzards in *nemoralis* from the digastric condition. The common ancestor of *excavata* and the *Digaster-Didymogaster* assemblage is computed to have had the dichogastrin condition of nephridia (single preseptal funnel on each side), retained as a plesiomorphy in *Digaster* but changing to the multifunnelled condition in *excavata*. Some trees from the larger data set nevertheless do associate *excavata* and *nemoralis* as sister-species within the *Digaster* assemblage.

The PAUP analyses are not sufficiently extensive to rule out the alternative possibility that *Perissogaster excavata* is descended from a monogastric megascolecin ancestor with its nephridial condition of multiple preseptal nephrostomes in caudal segments, conditions seen in *Oreoscolex* Jamieson. Two *Oreoscolex* species from New South Wales, *O. illawarrae* (Fletcher, 1889) and *O. saccarius* (Fletcher, 1886) agree with *P. excavata* in having the intestinal origin in XVI. However, confinement of multiplication of gizzards to a single zoogeographical province favours the view that multiplication is a rare apomorphy more likely to occur in closely related forms than in forms as distinct as *Oreoscolex*.

In view of the logical and computational ambivalence as to the position of *P. excavata* it is here considered that taxonomic convenience is best served by retaining this species in the monotypic genus *Perissogaster*. This has been redefined in the taxonomic section.

ACKNOWLEDGEMENTS

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ON THE ALLEGED OCCURRENCE OF THE EARLY CRETACEOUS AMMONITE *SIMBIRSKITES* IN QUEENSLAND

SIMON R.A. KELLY

Kelly, S.R.A. 1993 06 30: On the alleged occurrence of the Early Cretaceous ammonite *Simbirskites* in Queensland. *Memoirs of the Queensland Museum* 33(1): 245-251. Brisbane. ISSN 0079-8835.

The two ammonite specimens that comprise the Australian records of the Early Cretaceous genus *Simbirskites* are reassessed. Formerly described as *S. morvenae* Whitehouse, they are re-identified here as Late Jurassic, *Galbanites galbanus* Buckman and *G. fasciger* Buckman. The Australian specimens were supposedly from Queensland, but are believed here to be exotic, brought from England probably in the late nineteenth century. Their limestone lithology contrasts with the local clastic sediments. They closely resemble the form and lithology of specimens from the Portland Stone of England. Furthermore they are associated with gastropods, *Leptomaria rugata* (Benett), and bivalves including *Laevitrigonia damoniana* (de Loriol) and oysters which are also comparable to Portland Stone forms. Simbirskitids are typically boreal in their distribution, occurring in mid-Hauterivian to Early Barremian deposits in northern Europe, parts of the USSR and North America. Most other austral occurrences have been previously discounted. The geographically isolated Australian occurrence now should be deleted from the record. □ *Late Jurassic, Early Cretaceous, ammonite, bivalve, gastropod, Portland Stone, Simbirskites, Galbanites, England, Queensland, Australia.*

Simon R.A. Kelly, British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Rd, Cambridge CB3 OET, England; 21 August, 1992.

In the Queensland Museum type collection, I recognised a moderately large, English, Portland Stone ammonite in characteristic limestone preservation. On reading the label, I was surprised to discover that this was reputedly from the Queensland Early Cretaceous. A smaller ammonite and three large gastropod internal moulds have been artificially attached with cement to the umbilicus. The two ammonites were placed in *Simbirskites* (Whitehouse, 1926) without sighting the specimens (Bryan & Whitehouse, 1926). Whitehouse (1927) described the smaller, Queensland Museum (QM) F16438, as type of *S. morvenae* sp. nov.; the larger (QM F1270) was made paratype. The ammonites are re-identified here, the larger one as *Galbanites (Galbanites) galbanus* (Buckman), and the smaller one as *G.* (*G.*) *fasciger* (Buckman). The gastropods (QM F21078-21081) originally determined as *Leptomaria* (?) (Etheridge, 1909) are identified here as '*Leptomaria*' *rugata* (Benett). In the matrix, Whitehouse (1927) identified fragments of '*Ostrea*' and '*Trigonia*'. The oyster may be *Liostrea* sp.; other undetermined oysters, possibly exogyrids, grew on the interior of the body chamber of the larger ammonite shell. The trigoniid shows an early commarginal ribbed phase, followed by later somewhat irregular tuberculation typical of *Laevitrigonia damoniana* (De Loriol, 1875). '*Leptomaria*' *rugata, Liostrea,* exogyrids and *L. damoniana* are present in the English Portland Stone; the last is restricted to it and French stratigraphic equivalents. Stratigraphically, the youngest occurrences of *Laevitrigonia* s.s. are undescribed specimens in the Berriasian of the Russian Platform, and close to the Jurassic-Cretaceous boundary in the Cinder Beds of southern England (Kelly, 1988). It is unknown in the Hauterivian. However, it is well known in the Late Jurassic of northern and western Europe, and is particularly common in the Portlandian/Tithonian Portland Limestones of southern England.

The composite specimen was originally acquired from a Mr Hurst or Mr Hunter (Rozefelds et al., 1990) and was catalogued in the Queensland Museum as D7710.12 in 1893. The cited locality is 'Victoria Downs, Morven' where extensive outcrops of the marine, Aptian, Roma Series, are placed in the Doncaster Member of the Wallumbilla Formation (Exon, 1971). However, despite detailed geological survey work in the area, no further *Simbirskites*, nor specimens of similar lithology have been collected (Day, 1969: 152).

Etheridge (1909) originally compared the ammonites to *Perisphinctes kayseri* Neumayr & Uhlig (1881), now recognised as *Simbirskites*, which occurs in the *seeleyi* zone, Hauterivian, of north

Germany (Rawson, 1971). Whitehouse (1926, 1927) initially appeared to accept a Queensland provenance. Whitehouse (1946: 3) intimated that the ammonites were exotic, stating 'a little uneasiness is felt about the locality record' and that preservation of the specimens was like that of simbirskitids of north Germany which last remark is not supported here. Whitehouse (1954: 9 footnote) reiterated his belief of an extra Australian provenance. This remark was supported by Day (1969: 152). Lithologies of the large German simbirskitids figured by Neumayr & Uhlig are ironstones (Rawson, 1971), whereas most other German occurrences are from paralic sandstones or offshore clay facies. Sediments of the Wallumbilla Formation are predominantly sandstones with minor mudstones, but the specimens, supposedly from Morven, are preserved as internal moulds in a pale creamy brown limestone with much bioclastic debris. The preservation exactly matches that of parts of the English Portland Stone.

The Simbirskitinae is a boreal group of Olcostephanidae, one of the youngest in the once widespread Perisphinctoidea. It is characteristic of the mid-Hauterivian to earliest Barremian of northern England, northern Europe, the Russian Platform, Spitsbergen and North America (Rawson, 1971). Possible Late Valanginian forerunners occur in Arctic Canada (Jeletzky & Kemper, 1988).

The Australian record of *Simbirskites*, discounted here, has been widely quoted, (Wright in Moore, 1957). Other records of simbirskitids outside the normal geographical range for the group were reviewed by Rawson (1971). Mexican (Burckhardt, 1912) and Himalayan forms (Uhlig, 1910, were re-identified (*Grayiceras*) (Spath, 1924). Leanza (1958) described four species of *Simbirskites* from Argentina, but these appear to be *Rogersites*. Kilian & Piroutet (1905) recorded *Simbirskites* from New Caledonia, but the record remains unsubstantiated (Whitehouse, 1926).

SYSTEMATICS

Class CEPHALOPODA
Superfamily PERISPHINCTOIDEA
Steinmann, 1890
Family PERISPHINCTIDAE Steinmann, 1890
Subfamily DORSOPLANITINAE Arkell, 1950

Galbanites Buckman, 1922

Type species. Galbanites galbanus Buckman, 1922, Portland Stone, Haddenham, Buckinghamshire, England.

REMARKS

Arkell (in Moore, 1957) synonymized *Galbanites* and *Titanites* Buckman, 1921 but Wimbledon & Cope (1978) recognised *Galbanites* as distinct. The specimens described below as *Galbanites* have predominantly biplicate to triplicate ribbing, but lack the coarseness of the primaries which characterises *Galbanites* (*Kerberites*). The genus is widespread in the *okusensis* and *kerberus* Zones of southern England.

Galbanites (Galbanites) galbanus
Buckman, 1922 (Figs 1,2A,3)

1909 *Perisphinctes kayseri* Neumayr & Uhlig; Etheridge, p.239, pl.68 [larger specimen only; non Neumayr & Uhlig, 1881].
1922 *Galbanites galbanus* Buckman, pl.355, figs A,B,C.
1926 *Simbirskites* spp. Whitehouse, p.200 [larger specimen only].
1927 *Simbirskites morvenae* sp.nov. Whitehouse, p.111, paratype only [non pl.16, fig. 1; non text fig. 5].
1938 *Galbanites galbanus* Buckman; Roman, p.297.
1946 *Simbirskites*; Whitehouse, p.8.
1972 *Galbanites galbanus* Buckman; Clark, p.82.
1974 *Galbanites galbanus* Buckman; Wimbledon, p.146, pl. 18.
1978 *Galbanites galbanus* Buckman; Wimbledon & Cope, p. 184.
1990 *Simbirskites morvenae* Whitehouse; Rozefelds et. al, p.701.

MATERIAL EXAMINED

HOLOTYPE: British Geological Survey, GSM47155, Haddenham Micritic Member (Blue and Cream Bed, Creamy Limestone), Portland Stone, works north of the railway station, Haddenham, Buckinghamshire, England (Buckman, 1922)

OTHER MATERIAL: QM F1270, originally catalogued as D7710.12 in 1893 and stated to be from Victoria Downs, Morven, Queensland. Donated by Mr Hurst or Mr Hunter. The provenance is believed here to be from the English Portland Stone.

DIAGNOSIS

Evolute perisphinctid with coarse biplicate to triplicate ribbing, branching just below mid-flank (Fig. 1). Whorl section rounded (Fig. 2A). Ribbing gently arched forward to rectiradiate, with only weak forward swing over the venter. Shell

FIG. 1. *Galbanites* (*Galbanites*) *galbanus* Buckman, 1922. Lateral view of internal mould of QM F1270 (larger specimen), showing QM F16438 (smaller specimen, *G.* (*G.*) *fasciger* Buckman) artificially attached to the umbilicus, together with four internal moulds of gastropods, QM F21078-21081, '*Leptomaria*' *rugata* (Benett); ×0.5. (See also Figs 2,3 for further detail).

septate up to a diameter of 330mm. Body chamber outer two thirds whorl; aperture not seen; suture in Fig. 3. Maximum diameter 365mm; septate diameter 244mm; maximum whorl height 112mm, width 85mm; no. of ribs 55 primary, 133±2 secondary.

REMARKS

The holotype of *Simbirskites morvenae* Whitehouse differs from the holotype of *Galbanites galbanus* Buckman by its larger size, and tendency towards triplicate as well as biplicate secondary ribs. It differs from *G. fasciger* by having rounded flanks, as opposed to flat sided, and the absence of fasciculation. *G. galbanus* occurs in the later *okusensis* and early to middle *kerberus* zones of southern England (Wimbledon & Cope, 1978).

Galbanites (Galbanites) fasciger Buckman, 1923 (Fig. 1, centre; Fig. 2, B,C,D).

1909 *Perisphinctes kayseri* Neumayr & Uhlig; Etheridge, 239, pl.68 [small specimen only; non Neumayr & Uhlig, 1881].
1923 *Galbanites fasciger* nov. Buckman, pl.451.
1926 *Simbirskites* spp. Whitehouse, p.200 [small specimen only].
1927 *Simbirskites morvenae* sp.nov. Whitehouse, p.111, pl.16, fig. 1; text fig. 5 only.
1946 *Simbirskites;* Whitehouse, p.8.
1972 *Galbanites fasciger* Buckman; Clark, p.82.

FIG. 2. A, *Galbanites* (*Galbanites*) *galbanus* Buckman, 1922, ventral aspect of QM F1270, ×0.5; B-D, *Galbanites* (*Galbanites*) *fasciger* Buckman, 1924; B, left lateral view, QM F16438, ×1. (Holotype of *Simbirskites morvenae* Whitehouse, 1926): C, right lateral view of QM F16438, ×1; D, ventral view of QM F16438, ×1.

1974 *Galbanites fasciger,* Buckman; Wimbledon, p.72.
1990 *Simbirskites morvenae* Whitehouse; Rozefelds et. al, p.701.

MATERIAL EXAMINED

HOLOTYPE: British Geological Survey, GSM37302, formerly S. Buckman Collection 295556, purchased 1924, 'Lower Witchett', Creamy Limestone, Portland Beds, Barrel Hill, Long Crendon, Buckinghamshire, England.

OTHER MATERIAL: QM F16438, cemented to umbilicus of QM F1270, information as for *G. galbanus* above.

DIAGNOSIS

Moderately involute perisphinctid (Fig. 2 B,C), with flattened, ventrally converging sides (Fig. 2D). Ribs straight and prorsiradiate, fasciculate, branching in mid- to just above the mid-flank into usually three secondary ribs. Intercalatory secondary ribs also present.

MEASUREMENTS

Maximum diameter 65mm; septate diameter 37mm; maximum whorl height 26mm, width 21mm; no of ribs c.27 primary, about 75 secondary.

FIG. 3. *Galbanites* (*Galbanites*) *galbanus* Buckman, 1922, internal mould showing detail of suture, QM F1270. At left are moulds of '*Leptomaria*' *rugata* (Benett, 1831) artificially cemented to the umbilicus. ×1.

REMARKS

The specimen of *G. fasciger* differs from *G. galbanus* by being smaller, more involute, flatter sided and having fasciculate ribs. The ribbing is more regularly prorsiradiate. Wimbledon (1974: 72) believed that *G. fasciger* represented the inner/juvenile whorls of *Briarites polymeles* Buckman or a closely related species.

Class GASTROPODA
Family PLEUROTOMARIIDAE Swainson, 1844

Leptomaria Eudes-Deslongchamps, 1864

Type species. Pleurotomaria amoena Eudes-Deslongchamps, 1849, Bajocian, Middle Jurassic, France.

'Leptomaria' rugata (Benett, 1831)
(Figs 1, 3) (Fig. 1, centre; Fig. 3, left)

1831 *Trochus rugatus* Benett, p.6, pl.16, upper right.
1888 *Pleurotomaria rugata* Benett; Damon, pl.8, fig. 6.
1909 *Leptomaria* (?) sp.; Etheridge, p.239, pl.68.
1927 *Leptomaria* (?) sp.; Whitehouse, p.111.
1946 *Leptomaria* (?) sp.; Whitehouse, p.3.
1989 *Trochus rugatus* Benett; Spamer, Bogan & Torrens, p. 141 [q.v. for further synonymy].

MATERIAL EXAMINED

SYNTYPE: Original of Benett (1831: pl.16) upper right figure, Academy of Natural Science, Philadelphia, 65710 (B.C. 506), fide Spamer et al. (1989), Portland Beds, Tisbury, Wiltshire.

OTHER MATERIAL: Four specimens: QM F21078-21081, artificially cemented to the umbilicus of QM F1270.

REMARKS

The smooth internal moulds have the apices broken off, but would have had a blunt apical angle; there are traces of a weak shoulder. The preservation is typical of '*L.*' *rugata* in the Portland Beds of England.

CONCLUSIONS

The two ammonites, reported to be from the Early Cretaceous of Victoria Downs, Queensland, formerly attributed to Hauterivian *Simbirskites* (Whitehouse, 1926, 1927, 1946), are confirmed, along with associated bivalves and gastropods, as English, Late Jurassic, Portland Stone forms. *Galbanites* (*Galbanites*) *galbanus* and *G.* (*G.*) *fasciger* suggest Portlandian/Tithonian faunas 3/4, the *okusensis/kerberus* zones of Wimbledon & Cope (1978) and Cope et al. (1980). The Cockly Bed of the former Okus Quarry in Swindon, Wiltshire, is probably the most likely original site, but is not proven. The gastropod '*Leptomaria*' *rugata* and the bivalves, including *Laevitrigonia damoniana* and oysters associated with the ammonites are also common in the Cockly Bed. The record of *Simbirskites* from Australia should now be deleted. The provenance of other material of the Hurst/Hunter bequest should be treated with caution.

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NEW INFORMATION ON THE AUSTRALIAN SMALL BITTACIDS (MECOPTERA)

KEVIN J. LAMBKIN

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The unrecorded male and additional females of the small and little known scorpion-fly *Symbittacus scitulus* Byers have been found at three north Queensland montane rainforest localities. The male terminalia are similar to those of *Edriobittacus* Byers. New localities for the other small Australian bittacids show that *Austrobittacus anomalus* Riek occurs in the coastal zone between Bundaberg and Rockhampton, *Tytthobittacus macalpinei* Smithers extends into south-east Queensland, and *Edriobittacus microcercus* (Gerstaecker) is widely distributed between Bundaberg and Cairns. □ *Mecoptera, Bittacidae, Edriobittacus, Tytthobittacus, Austrobittacus, scorpion-fly, rainforest, Queensland, new records.*

Kevin J. Lambkin, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 6 November, 1992.

The Australian bittacid fauna comprises 6 genera. The monotypic *Austrobittacus* Riek, *Edriobittacus* Byers, *Symbittacus* Byers and *Tytthobittacus* Smithers are small and delicate forms, which have AA_{3+4} (=*1A* of other notations) of the hindwing much reduced. *Bittacus* Latreille (1 species) and *Harpobittacus* Gerstaecker (9 nominal species) are large and robust scorpionflies with AA_{3+4} of the hind wing well developed. Byers (1986) provided a key to all genera except *Bittacus*, which was differentiated by Lambkin (1988).

Symbittacus was erected by Byers (1986) for *S. scitulus* Byers, which was based on one female from rainforest of Bellenden-Ker Range, north Queensland. Since then, further collecting by G.B. Monteith and colleagues in montane rainforest south of Bellenden-Ker has brought to light a further five specimens, including the first male. An examination of the collections of the Australian National Insect Collection, Canberra (ANIC) has also revealed a female specimen from another north Queensland rainforest locality. Herein I record this new material and describe the male. As well, new diagnostic characters and new localities are given for *Austrobittacus*, *Edriobittacus* and *Tytthobittacus*. No new localities have been published for these taxa since their original descriptions or since Riek (1954). Full reference lists for each have recently been given by Smithers (1987) and are not repeated here.

All measurements are in millimetres. Other abbreviations used are as follows: ICZN, International Code of Zoological Nomenclature; KJL, author's collection (to be deposited in Queensland Museum); LFW, fore wing length; MV, Museum of Victoria, Melbourne; QM, Queensland Museum, Brisbane; UQ, The University of Queensland Insect Collection, Department of Entomology, University of Queensland.

Symbittacus scitulus Byers
(Figs 1A-C,2)

Symbittacus scitulus Byers, 1986, pp. 166-168, figs 1-6.

MATERIAL EXAMINED

QUEENSLAND: QM: 1♂,1♀ (both teneral), Cardwell Range, Upper Broadwater Ck valley, 700-800m, RF [rainforest], 17-21.xii.1986, 3♀♀, Kirrama Range, Douglas Ck road, 800m, 9-12.xii.1986, all G.Monteith, G.Thompson and S.Hamlet. ANIC: 1♀, Davies Ck, 20km E by S Mareeba, 20.xi.1981, D.H.Colless, Malaise trap.

LFW

♂ 14.9, ♀♀ 14.1-14.6 (holotype recorded by Byers (1986) as 14.1).

MALE TERMINALIA (Fig.1A-C)

Epiandrium short, plate-like, articulated on the anterodorsal corners of sternum 9; in lateral view (Fig.1A) narrow, arched dorsally at c.⅔ length; in dorsal view (Fig.1B) posterior margin broadly incised to c.⅔ length, resultant lobate paired lateral regions each with 5 short black spines medioapically. Posterior margin of sternum 9 with a few long setae dorsally. Basistyles completely fused medially; in lateral view ventroposterior margin evenly curved; dististyle-bearing lobes strongly produced. Dististyle (Fig.1C) small and simple, with strongly sclerotised glabrous apical knob; distinct 'stylocavernula' (Tjeder 1970) basally. Aedeagus of moderate length, recurved, without a terminal

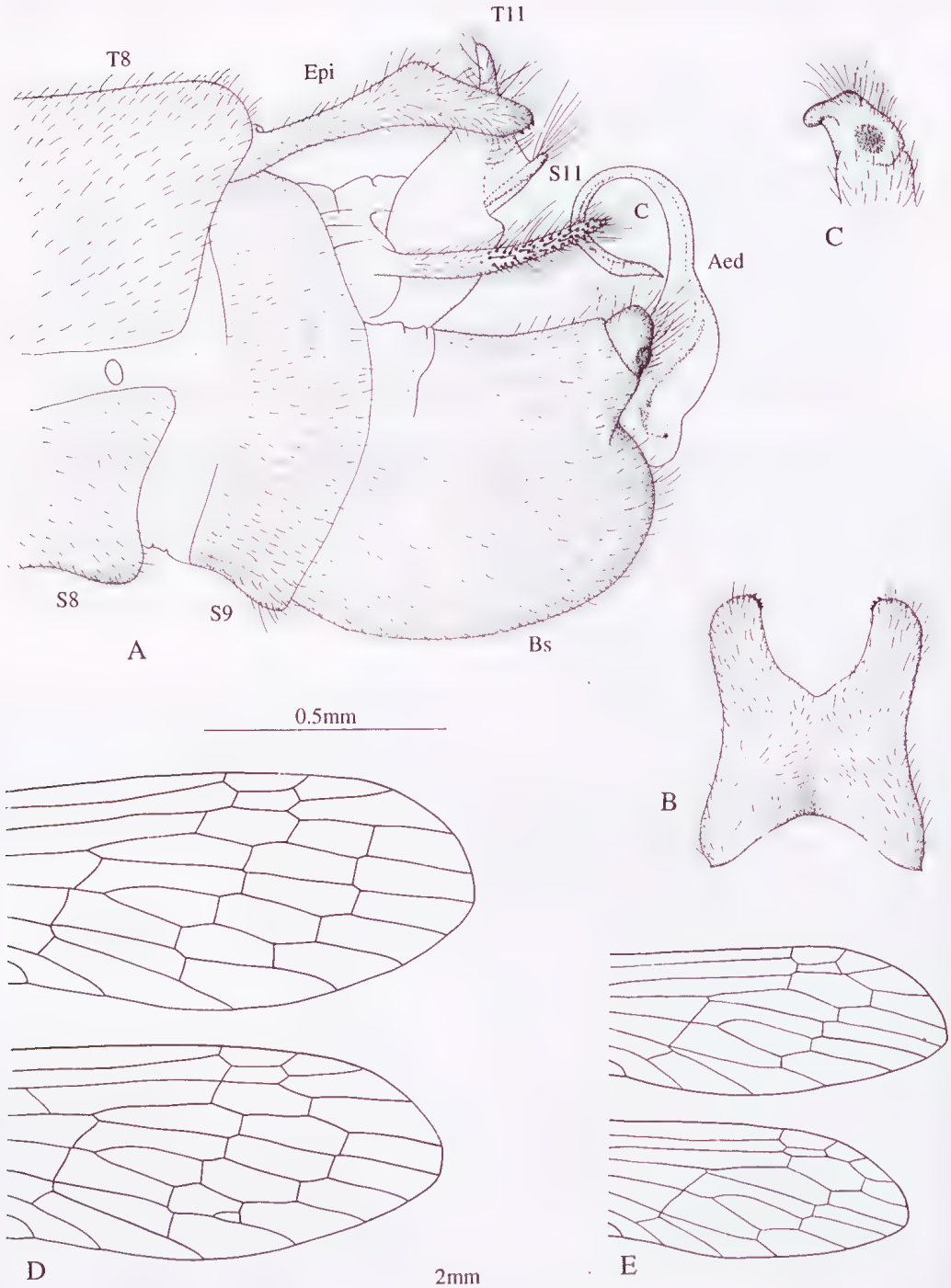

FIG. 1. A-C (0.5mm scale line). *Symbittacus scitulus*, male: A, apex of abdomen, left lateral; B, epiandrium dorsal; C, right dististyle, posteroventral (darker circular area is the 'stylocavernula'). D,E (2mm scale line Distal regions of right fore and hind wings (venation only shown): D, *Edriobittacus microcercus*; E, *Tytthobi tacus macalpinei*. Abbreviations: Aed, aedeagus; Bs, basistyles; C, cercus; Epi, epiandrium; S8,9,11, stern 8,9,11; T8,11, terga 8,11.

filamentous extension. Tergum 10 not detected (specimen teneral). Cercus elongate, reaching to level of dististyle; broadest at c.½ length, then tapering distally. Tergum 11 elongate, in posterior perpendicular view tapering to an acute apex. Sternum 11 much shorter than tergum 11, with apical margin truncate.

REMARKS

The new material compares well with Byers' (1986) description, but 2 minor variances can be noted. Byers recorded the ocelli as of uniform diameter. In all the new material (and, on re-examination, in the holotype as well) the lateral ocelli are slightly larger than the medial one. The number of thick black setae on each side of the 4th hind tarsomere, recorded as 1 by Byers, is variable. The holotype and one of the Kirrama females (both with fore wings 14.1 long) have 1 or 2, whereas the other specimens (which are larger) have 2. Unfortunately the male is teneral and not well preserved, but its non-genitalic structural features are similar to those of the female.

The male terminalia of *S. scitulus* are similar to those of *Edriobittacus microcercus* (Gerstaecker) (Byers, 1974, figs 1-3). The latter differ, however, in the following: 1, the epiandrium in lateral view is arched before midlength (at c.⅔ length in *Symbittacus*), and more strongly so than in *Symbittacus*; in dorsal view it is much more deeply incised than in *Symbittacus*; 2, the aedeagus is longer; 3, there are numerous (rather than a few as in *Symbittacus*) long setae on the posterior margin of sternum 9; 4, tergum 11 is short with the apical margin truncate (elongate with apex acute in *Symbittacus*).

Symbittacus scitulus is a rainforest scorpionfly. It has only been taken at elevations of 700-800m. The specimens from Cardwell and Kirrama Ranges were collected at night while at rest on the foliage of understorey vegetation along tracks through rainforest (G.B. Monteith, pers. comm.).

Austrobittacus anomalus Riek
(Fig. 2)

Austrobittacus anomalus Riek, 1954, p.157, figs 3,4, pl.1, fig.6.

MATERIAL EXAMINED

QUEENSLAND: ANIC: holotype ♂, allotype ♀, 1 without abdomen, 4♂♂ and 10♀♀ paratypes, Rockhampton, 23.iii.1950, 1♀ paratype, Olsen's Caves, 13 miles N Rockhampton, 25.iii.1950, all I.F.B.Common; 1♂, 3♀♀, Pine Ck, 12 miles S Bundaberg, 12.iii.1976, 14.iv.1976, 1♂, Monduran Dam, 20km N Gin Gin, 2.ii.1974, all H.Frauca. KJL: 5♂♂, 6♀♀, Bruce Highway, Rosedale turnoff, 10km NW Gin Gin, 4♂♂, 6♀♀, near 'Wakelin', 20km NNW Gin Gin, all 20.iv.1985, K.J. and C.L.Lambkin.

LFW

♂♂ 14.0-15.3, ♀♀ 13.8-14.6 (Riek (1954) recorded 15.0 for the species).

REMARKS

Riek (1954) did not explicitly state which specimens were the holotype, allotype or paratypes. The holotype and allotype are labelled as such, but none of Riek's other specimens are labelled as paratypes. Riek did not, however, expressly exclude any of his specimens from the

FIG. 2. Distribution of *Symbittacus scitulus* and *Austrobittacus anomalus*.

type series (see ICZN Article 72(b)(i)), and I believe that there is sufficient evidence (see ICZN Recommendation 72B) to regard the 16 specimens listed above as paratypes (viz the collection data match those given by Riek, and the Olsen's Caves specimen matches that illustrated by Riek (1954, pl.1, fig.6) and stated to be a paratype in the figure caption).

This species is easily distinguished by the longitudinal form of the free apical portion of AA_{3+4} in the hind wing (Byers, 1991, fig.37.6C). The lateral ocelli are slightly larger than the medial one. The number of thick black setae on each side of the 4th hind tarsomere, recorded by Byers (1974) as 4-5, ranges from 2 to 7 and can vary from side to side in the same specimen.

All specimens have been taken in late summer or autumn. The Rosedale turnoff and Wakelin specimens were collected in the grass understorey of eucalypt woodland in company with *Edriobittacus microcercus* (at Wakelin only) and *Harpobittacus scheibeli* Esben-Petersen.

FIG. 3. Distribution of *Edriobittacus microcercus* and *Tytthobittacus macalpinei*.

Edriobittacus microcercus (Gerstaecker) (Figs 1D,3)

Bittacus microcercus Gerstaecker, 1885, p.119.
Kalobittacus microcercus: Riek, 1954, pp.155-156, figs 1,2.
Edriobittacus microcercus: Byers, 1974, pp.165-167, figs 1-4.

Material Examined

Queensland: ANIC: 1♂, 12 miles E Duaringa, 18.iii.1958, 4♂♂, 1♀, 25 miles N Gin Gin, 16(1♂) and 23.iii.1958, 2♂♂, 1♀, Hedlow Ck, nr Yeppoon, 22.iii.1958, all I.F.B.Common; 1♀, Ingham, 29.iii.1961, K.L.S.Harley; 1♂, Mackay, 17.v.1969, [G.F.] Bornemissza, 'flew to light'; 1♀, 63 miles N Marlborough, 9.v.1955, K.R.Norris; 1♂, Olsen's Caves, 13 miles N Rockhampton, 25.iii.1950, I.F.B.Common; 1♂, Palm Grove [?Cove], nr Cairns, June 1969, R.Hardie; 1 without abdomen, Pine Ck, 12 miles S Bundaberg, 12.iii.1976, 1♀, Pinock R, Hogback Range, WSW Bundaberg, via Gin Gin, 11.iii.1972, all H.Frauca; 1♀, 7 miles NNE Ravenshoe, 3300', 22.iv.1969, I.F.B.Common and M.Upton; 1 without abdomen, Rockhampton; 1♂, The Caves, 16 miles N Rockhampton, 3.iv.1967, M.S.Upton. KJL: 1♂, near 'Wakelin', 20 km NNW Gin Gin, 20.iv.1985, K.J. and C.L.Lambkin. UQ: 1♀, Walkamin, Atherton Tableland, August 1967, P.H.Twine. MV: 3♂♂, 3♀♀, 1 without abdomen, 'Queensland'.

LFW

♂♂ 16.3-19.7 (holotype recorded by Esben-Petersen (1921) as 18.0), ♀♀ 17.1-19.5

Remarks

Both sexes have the lateral ocelli much larger than the medial one (noted in the male only by Byers, 1974), and the number of thick black setae on each side of the 4th hind tarsomere, recorded by Byers (1974) as 3, ranges from 2 to 5.

The holotype was from Peak Downs. The only other previous records are those of Riek (1954): the Olsen's Caves specimen in the ANIC, and the series labelled 'Queensland' in the MV. All specimens have been taken from March to August.

Tytthobittacus macalpinei Smithers
(Figs 1E,3)

Tytthobittacus macalpinei Smithers, 1973, p.300, figs 9-11.

MATERIAL EXAMINED

NEW SOUTH WALES: KJL: 1♂, Terania Ck, 22.i.1986, L.Müller and G.Theischinger. QUEENSLAND: UQ (all in poor condition): 1♂, 1♀, Brisbane, 8.x.1959, F.Lamberth, 9.x.1966, E.Rainey; 1♀, Kenilworth State Forest, 5.xii.1966, G.B.Monteith, 'sweeping ferns in rainforest'; 1♂, Mt Coot-tha, Brisbane, 26.ix.1959, A.J.Jackson.

LFW

Terania Ck ♂13.3 (Smithers, 1973, recorded 14.0 for the species).

REMARKS

T. macalpinei is very similar in wing venation to *E. microcercus*. Further to Byers (1986), it can be distinguished by its smaller size (LFW c.13.0-14.0, vs at least 16.3 in *E. microcercus*) and two series of crossveins in the distal region of both wings (Fig. 1E) compared to three in *E. microcercus* (Fig. 1D). The latter character is particularly useful in identifying faded or teneral females, which Byers' key will not separate. The lateral ocelli are slightly larger than the medial one and there are 1-3 thick black setae on each side of the 4th hind tarsomere.

Smithers' (1973) material was all from New South Wales: Huonbrook, Mooney Mooney Creek, Mt Wilson and Wentworth Falls. The Terania Creek and Kenilworth specimens were both taken in rainforest, the former in flight along a creek bed (G. Theischinger, pers. comm.) and the latter swept from ferns. The records from Brisbane and Mt Coot-tha, not obvious rainforest localities, are based on student collections and could be doubtful. All specimens have been taken from September to March.

ACKNOWLEDGEMENTS

I appreciate the cooperation of Josephine Cardale (ANIC), Ken Walker (MV) and Margaret Schneider (UQ) in making available specimens under their care. Christine Lambkin drew Fig. 1A-C for which I am very grateful.

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MIDDLE TRIASSIC ORTHOPTEROID (TITANOPTERA) INSECT FROM THE ESK FORMATION AT LAKE WIVENHOE. *Memoirs of the Queensland Museum 33(1): 258. 1993:-* This large insect wing was collected from plant fossil-rich siltstone in an old road cutting near 5 Mile Creek on the western shore of Lake Wivenhoe (GR523792 on Caboolture 1:100000 topographical sheet No.9443 (1972)), approximately halfway between the dam wall and Esk, by Leon Steinhardt in 1991. These siltstones of the Esk Formation contain a typical *Dicroidium* megaflora and an early Middle Triassic (Anisian) palynoflora (deJersey, 1972).

It is the first insect from this formation and first Queensland record of the Titanoptera; *Clatrotitan* McKeown,1937 (see Riek,1954) from the Middle Triassic of Brookvale, NSW is the only other Australian record.

The shape does not match other members of the order and this is thought to be due to preservation. A piece of fern stem, adjacent to the rear margin in the Cu and A regions, could have snagged the wing floating on a few millimetres of water. If the wind direction was from the anterior of the wing this may have swung the distal third of the wing retrally, giving the unusual shape to the anterior margin and could have crumpled the anterior marginal areas.

Order TITANOPTERA Sharov,1968

The new wing conforms in most respects with Kukalová-Peck's (1991) ground plan for this order: M with a long stem, adjacent to R; Cu not stemmed, CuA adjacent to M basally, diverging before M divides, then connected to CuP1+2 by a strut; CuP deeply forked; AA2 simple. It is, however, in the form of MA, MP, CuA, CuP1+2 and CuP3+4, very different from known species and probably represents a new family.

Because the veins are directed towards the hind rather than apical margin and RP occupies a relatively large area, it is considered a hindwing.

Steinhardtia gen.nov.

Type species. Steinhardtia maryae sp. nov.

Diagnosis. Large wing (>40mm long); primary R fork well beyond that of M; RA, RP, MA, MP, CuA, CuP1+2 and CuP3+4 all deeply dichotomously forked; RA with 4 major branches, RP with 6, MA with 8, MP with 2, CuA with 4, CuP1+2 with 3 and CuP3+4 with 5; strut from CuA to CuP1 rather than CuP1+2; first branch of AA3+4 apparently dichotomous; cellular network between veins absent or not preserved.

Remarks. In the hindwings of other genera (Sharov, 1968) the primary R fork is closer to that of M, RP is usually pectinate, and MA. MP, CuA, CuP1+2 and CuP3+4 are simple for most or all of their lengths, and when forked have few branches.

Steinhardtia maryae sp.nov. (Fig.1)

Etymology. For the collector's wife, Mary.

Material. Holotype Queensland Museum F25507a and b.

Description. Incom plete hindwing, 40 × 10mm max dimensions, basal : nd fore marginal areas not preserved. Crossveins between RA and RP, and CuP1+2 and CuP3+4 as illustrated.

Remarks. The wing has been flattened so there is no convexity to any vein and this has probably obliterated any cellular venation between the main veins.

Acknowledgements

We are grateful to Leon Steinhardt for donating this fossil and to Sybil Monteith for the drawing.

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Peter A. Jell and Kevin J. Lambkin, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 18 December, 1992.

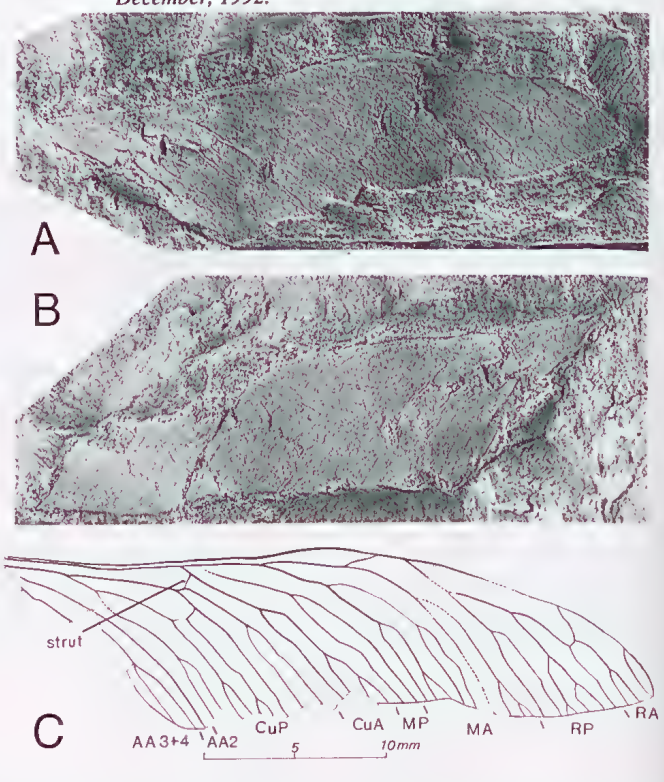

Fig. 1. *Steinhardtia maryae* sp.nov. A,B, holotype part and counterpart, × 1.8. C, venation diagram, notation following Kukalová-Peck (1991).

FREQUENCY OF OBSERVATION OF BIRD SPECIES IN SUB-COASTAL FARMLAND IN SOUTHEAST QUEENSLAND

G.J. LEACH AND H.B. HINES

Leach, G.J. & Hines, H.B. 1993 06 30: Frequency of observation of bird species in sub-coastal farmland in southeast Queensland. *Memoirs of the Queensland Museum* 33(1): 259-275. Brisbane. ISSN 0079-8835.

A farming district in southeast Queensland was surveyed from June 1980 to May 1985 to determine presence of bird species. Softwood scrub was the predominant vegetation before European settlement, but now occurs only in isolated remnant patches. Standard surveys were conducted on 20 days, one per season per year, and other surveys on another 100 days. The district supports a diverse and abundant avifauna: 44 waterbird, 60 non-passerine landbird and 88 passerine species.

Nearly 40% of waterbird and passerine species observed in standard surveys were observed in over 80% of them, but only 21% of non-passerine landbird species. In contrast, 45% of the latter species were observed on 20% or fewer visits, compared with 25% of the waterbird and passerine species. Frequency of several waterbird species was minimum in the wettest year, following widespread drought in southeast Australia.

Thirty species had large differences in mean seasonal frequency; some were summer or winter visitors. Approximate dates of presence are given. Rose Robin, Grey Fantail and Yellow-faced Honeyeater were present during well-defined winter periods, while Rufous Fantail and several other species were summer visitors. Scarlet Honeyeater and Spotted Pardalote were passage migrants.

The combination of standard and other surveys generated a robust database against which changes in relative abundance can, and should, be monitored to guide management. While an effective habitat mosaic remains for passerines and waterbirds, it appears less suitable for non-passerine landbirds other than doves and parrots which can be commensal with farming. Retention and better management of native woody vegetation may be essential to forestall decline in the avifauna with more intensive settlement. ☐ *Bird, farmland, habitat, remnant vegetation, seasonal movement, management.*

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Since European settlement, the vegetation of Australia has been progressively cleared and modified. This has led to decreases and actual losses of fauna and flora (Saunders, 1989; Hobbs & Hopkins, 1990; Recher & Lim, 1990; Saunders & Curry, 1990). Despite these changes, agricultural landscapes may be significant wildlife habitats (Breckwoldt, 1983, 1986; Saunders et al., 1987). Remnant vegetation along roadsides, for example, is used by many species of birds (Arnold & Weeldenburg, 1990; Cale, 1990; Saunders & de Rebeira, 1991; Leach & Recher, 1993).

Various workers have reported census data from avian communities in relatively undisturbed forest, woodland and heathland (e.g. Kikkawa, 1982; Pyke, 1983, 1988; Recher et al., 1985; Ford et al., 1985; Gosper, 1992; see also Keast et al., 1985; Ford, 1989). By contrast, information from highly modified landscapes is often anecdotal (e.g. Barnard, 1925; Lord, 1956) and comparisons of historical and present day abundances based on 'reporting rates' (Blakers et al., 1984) are insufficient for the needs of management because the data are compiled at too coarse a scale (Ford, 1989).

In this paper, we report five years of census data from the Marburg district, a subcoastal farming area of southeast Queensland. The district includes a diverse mosaic of habitats and is rich in bird species (Leach & Hines, 1987). The data concern (1) the relative abundances of bird species and (2) seasonal changes in their abundances. They provide a baseline that will permit assessment of future changes in the avifauna as land management practices alter or intensify.

English names for birds follow those of R.A.O.U. (1978).

STUDY AREA AND METHODS

The survey area

The survey area was the 10′ grid square centred on 27°35′S, 152°35′E (Fig 1a). Marburg is near the centre and Rosewood, with a population of

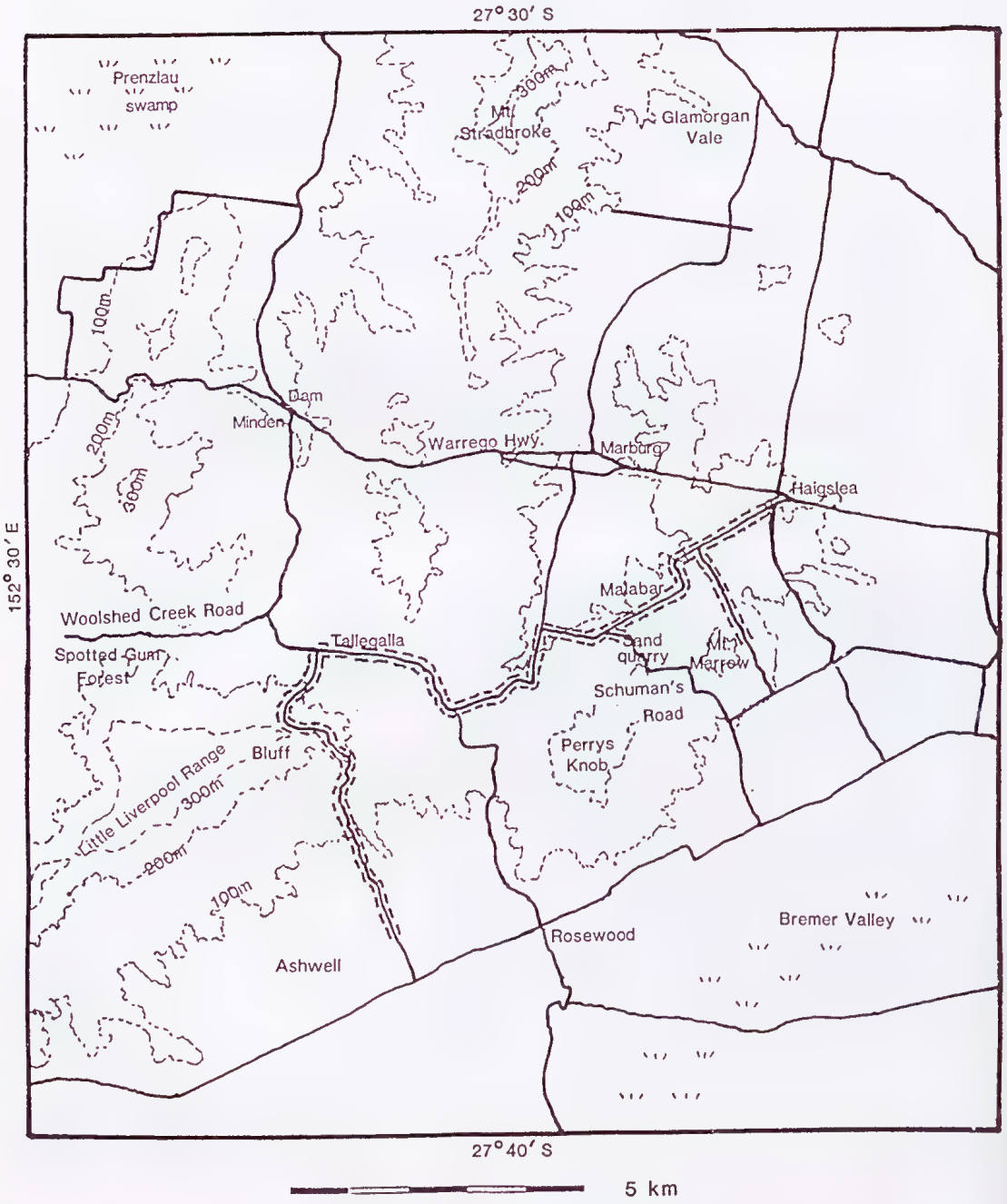
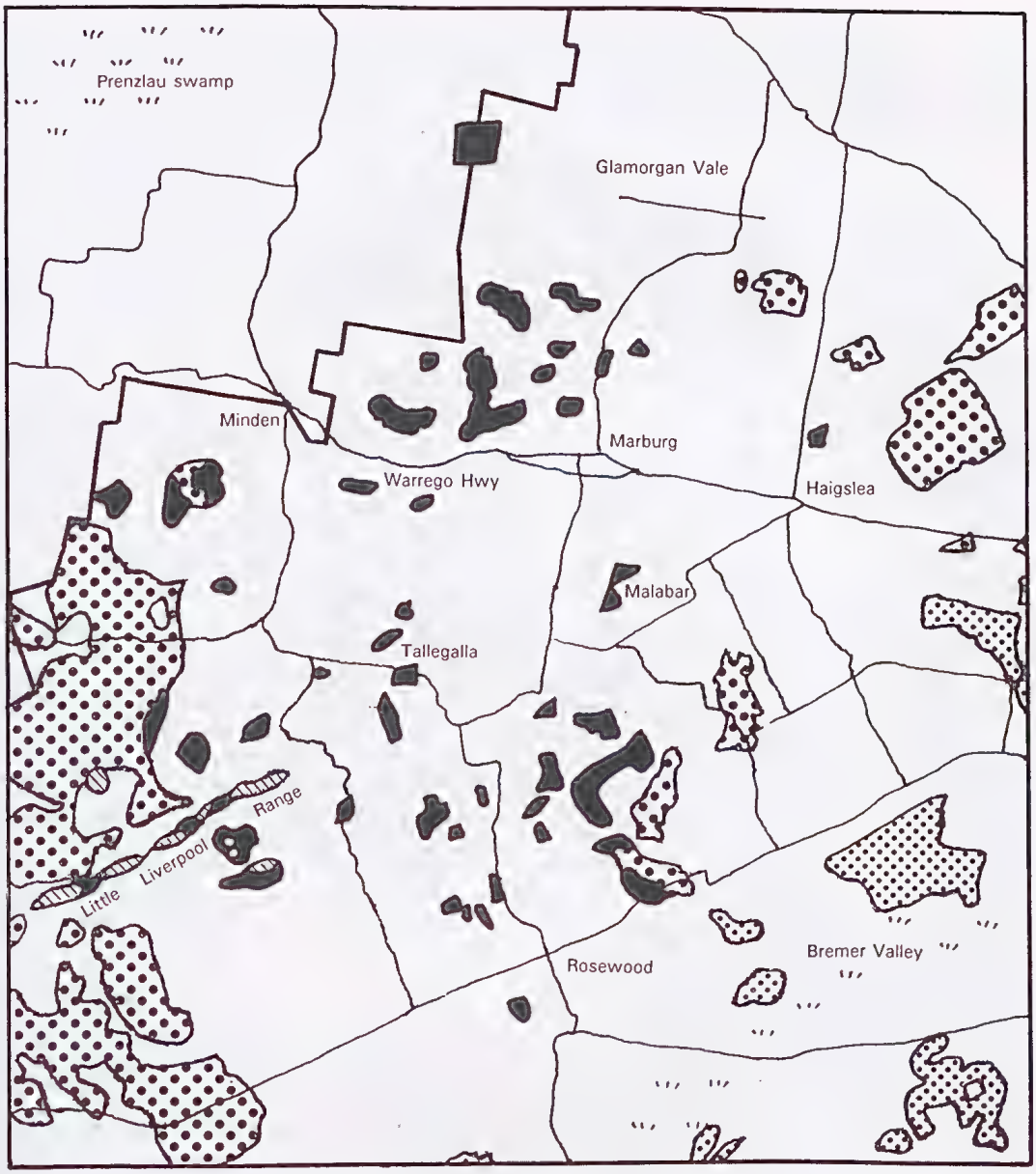


FIG. 1. The Marburg district showing (this page) the standard survey route (⁻⁻⁻), physiography and other features mentioned in the text and (next page) remnants of forest and woodland vegetation in the area of the grid square within Moreton Shire (after Young, 1985, courtesy of P.A. Young and Moreton Shire Council). An equivalent map is not available for the area beyond the shire boundary (the heavy line in the north-west) but distribution of vegetation remnants through the landscape, excluding the ephemeral swamp at Prenzlau, is not markedly dissimilar. Note that the widespread narrow galleries of vegetation along roadsides and fencelines are not shown.



Brigalow-softwood closed-forest.

Softwood-Hoop Pine (*Araucaria cunninghamii*) closed forest.

Eucalypt open-forest (Spotted gum, ironbarks; Gum-topped Box, *E. moluccana*, northeast of Haigslea).

Eucalypt woodland (Blue Gum, *E. tereticornis*, and ironbarks).

TABLE 1. Mean seasonal frequency (MSF) in standard surveys, and mean annual frequency (MAF) in standard surveys and other surveys, for waterbird species. Species are tabulated in descending order of MAF first in the standard surveys and subsidiarily in other surveys. Seasons are: Wi, winter; Sp, spring; Su, summer; Au, autumn. Range, the difference between maximum and minimum annual frequency. Years, the number of years, in parentheses, in which species were observed.

Species	Standard surveys							Other surveys		
	Wi	Sp	Su	Au	MAF	Range	Years	MAF	Range	Years
Australasian Grebe	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.98	0.11	(5)
Pacific Black Duck	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.96	0.11	(5)
Dusky Moorhen	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.95	0.12	(5)
Cattle Egret	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.91	0.15	(5)
Little Pied Cormorant	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.86	0.07	(5)
Eurasian Coot	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.83	0.35	(5)
White-faced Heron	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.80	0.37	(5)
Masked Lapwing	1.00	0.80	1.00	1.00	0.95	0.25	(5)	0.92	0.15	(5)
Little Black Cormorant	0.80	1.00	1.00	1.00	0.95	0.25	(5)	0.82	0.26	(5)
Purple Swamphen	1.00	1.00	0.80	1.00	0.95	0.25	(5)	0.79	0.32	(5)
Grey Teal	1.00	0.80	1.00	0.80	0.90	0.25	(5)	0.58	0.36	(5)
Hardhead	1.00	1.00	1.00	0.60	0.90	0.25	(5)	0.53	0.56	(5)
Straw-necked Ibis	0.80	0.60	0.80	1.00	0.80	0.50	(5)	0.74	0.55	(5)
Black-winged Stilt	0.60	0.60	0.80	0.60	0.65	0.25	(5)	0.47	0.53	(5)
Royal Spoonbill	0.60	0.60	0.80	0.60	0.65	1.00	(4)	0.35	0.46	(5)
Black-fronted Plover	0.60	0.80	0.60	0.60	0.65	0.75	(5)	0.28	0.48	(5)
Intermediate Egret	0.80	0.60	0.60	0.40	0.60	1.00	(4)	0.56	0.37	(5)
Pacific Heron	0.80	0.20	0.60	0.40	0.50	0.50	(5)	0.42	0.42	(5)
Comb-crested Jacana	0.60	0.40	0.40	0.60	0.50	0.75	(4)	0.33	0.67	(5)
Sacred Ibis	0.20	0.20	0.60	0.80	0.45	0.75	(4)	0.46	0.47	(5)
Maned Duck	0.60	0.40	0.40	0.40	0.45	0.50	(5)	0.40	0.17	(5)
Plumed Whistling-Duck	-	0.60	0.40	0.60	0.40	0.75	(3)	0.34	0.46	(5)
Latham's Snipe	-	0.80	0.80	-	0.40	0.50	(4)	0.24	0.26	(5)
Great Egret	0.40	0.60	-	0.20	0.30	0.75	(3)	0.39	0.42	(5)
Yellow-billed Spoonbill	0.40	-	0.20	0.20	0.20	0.25	(4)	0.27	0.51	(5)
Darter	0.20	-	0.20	0.40	0.20	0.50	(3)	0.14	0.14	(5)
Red-kneed Dotterel	0.20	0.20	0.20	0.20	0.20	0.75	(2)	0.10	0.28	(3)
Pink-eared Duck	0.20	0.40	-	0.20	0.20	0.50	(3)	0.07	0.16	(4)
Glossy Ibis	-	0.20	0.20	-	0.10	0.25	(2)	0.19	0.56	(3)
Little Egret	0.20	-	0.20	-	0.10	0.25	(2)	0.05	0.17	(3)
Australian Pelican	0.20	-	-	-	0.05	0.25	(1)	0.13	0.19	(4)
Great Cormorant	-	-	-	0.20	0.05	0.25	(5)	0.02	0.06	(5)
Black Swan	-	-	-	-	-	-		0.19	0.61	(4)
Australasian Shoveler	-	-	-	-	-	-		0.10	0.33	(4)
Little Bittern	-	-	-	-	-	-		0.06	0.07	(5)
Rufous Night Heron	-	-	-	-	-	-		0.03	0.06	(3)
Sharp-tailed Sandpiper	-	-	-	-	-	-		0.03	0.16	(1)
Whiskered Tern	-	-	-	-	-	-		0.03	0.11	(2)
Black-necked Stork	-	-	-	-	-	-		0.02	0.06	(2)
Wandering Whistling-Duck	-	-	-	-	-	-		0.02	0.05	(2)
Chestnut Teal	-	-	-	-	-	-		0.02	0.11	(1)
Buff-banded Rail	-	-	-	-	-	-		0.02	0.05	(2)
Pied Cormorant	-	-	-	-	-	-		0.01	0.06	(1)
Painted Snipe	-	-	-	-	-	-		0.01	0.06	(1)

1657, is the main town. Physiography, vegetation and land use are described by Leach & Hines (1987). The landscape, of low hills (max elevation: 396m) and broad valleys, has been substantially cleared for agriculture, other rural use and residential occupation. There are creeks that flow intermittently, small swamps and numerous farm dams.

Fertile prairie soils and grey cracking clays are common. In the past they supported low closed-forest and brigalow (*Acacia harpophylla*)-softwood closed-forest which covered about half the survey area (Anonymous, 1974; Young, 1985; Hass, 1987; Young & McDonald, 1987; Elsol, 1991). We describe these two vegetation types as softwood scrub; remnants are now patchily distributed and occupy less than 4% of the area (Fig. 1b). Many of the remnants are substantially disturbed. Thin solodic soils on some low hilly terrain support open eucalypt forest (Spotted Gum, *Eucalyptus maculata*, and the ironbarks *E. crebra* and *E. melanophloia* are common); these associations now cover about 9% of the district.

WEATHER

Weather records for Lawes, 15km west of the survey area, show a mean annual rainfall of 780±183mm (83 years) with 70% falling in October through March (Cook & Russell, 1983; Willcocks & Young, 1991). Mean monthly maximum temperatures range from 20.3°C in July to 31.0°C in December, and mean monthly minimum temperatures from 5.6°C in July to 19.1°C in February. On average, light frosts (screen minimum 0.1 to 2.2°C) occur on 12.5 days and heavy frosts (screen minimum 0.0°C or lower) on 2.3 days per year.

Between 1980 and 1985 annual rainfall (June through May) ranged from 697mm to 951mm. Seasonal variability was high with 23mm in June through August 1982 and 419mm in December through February 1981-82. In most seasons rainfall was near or below average but in March through May 1983, and June through August 1983 and 1984, rainfall exceeded the average by over 50% (Leach & Hines, 1992). Mean maximum monthly temperatures were >1°C above average from August through November 1980, in February and March 1983, in December 1984 and in January 1985 and were >1°C below average from September through November 1984. Minimum temperatures were >1°C above average from November 1981 through January 1982 and from May through October 1983 and were >1°C below average in June and July 1982. From June through August there were 17 light, and five severe, frosts in 1982, 11 light frosts in 1981, six in 1980 but only two in both 1983 and 1984.

SURVEY PROCEDURES

From June 1980 through May 1985 we surveyed birds along a standard route once each season (20 standard surveys). (Seasons are as follows: winter, June through August; spring, September through November; summer, December through February; autumn, March through May). The 20km route, from Haigslea to Ashwell (Fig 1a), was traversed between 0730 and 1200h. At eight sites foot surveys of 10 to 45 minutes were conducted (Appendix 1); additional observations were made during the 5 to 15 minute periods driving between sites. Mid-afternoon surveys of Minden Dam and its surrounds (Fig. 1a) were included in the standard survey. Surveys were conducted by two to four observers who listed all species of bird seen or heard. The main habitats sampled were open farmland (predominantly pasture with isolated acacia and other trees), degraded softwood scrub remnants, woody weeds along roadsides and fencelines, and farm dams.

In addition to the 20 standard surveys, the Marburg district was visited on another 100 days, usually between about 0700h and 1600h. Surveys conducted on these days are referred to as 'other surveys' though some wholly or partly overlapped the route of standard surveys. There were 18 visits in both winter and summer periods, 32 in both spring and autumn periods, and between 17 and 26 each year. Most observations were made while walking or driving slowly along secondary roads and bush tracks. G.J.L. was on all surveys and was usually accompanied by one or more experienced observers. Appendix 2 lists the principal areas visited, the frequency of visits and the main habitats represented. These surveys differed from the standard surveys in that eucalypt associations were often traversed.

DATA COLLATION

The likelihood that a species was present in the survey area was estimated for each species as: (number of visits on which the species was observed)/(total number of visits). Values were calculated for each season of each year (seasonal frequency) and for each year (annual frequency). Mean Seasonal Frequency (MSF) and Mean Annual Frequency (MAF) were derived from the five years of observations. Data from the standard surveys and from the other surveys are treated separately. Species with MAF>0.2 in the standard surveys are referred to as *principal* species. The difference between maximum and minimum annual frequency is used as a measure of variation across years. It is more useful than standard error, especially when means are based on observations from only one or two years.

In this report, waterbirds include all species of Podicipedidae, Pelecanidae, Anhingidae, Phalacrocoracidae, Ardeidae, Ciconidae, Plataleidae, Anatidae, Rallidae, Jacanidae, Rostratulidae, Charadriidae, Recurvirostridae, Scolopacidae and Laridae. Other non-passerines are referred to as non-passerine landbirds.

RESULTS

SPECIES OBSERVED

One hundred and thirty one species were observed in the standard surveys and 190 in other surveys (Tables 1-3). All species observed in the standard surveys, except Rose-crowned Fruit-Dove and Forest Kingfisher, were also observed in the other surveys. Thus, the total number of

TABLE 2. Mean seasonal frequency (MSF) in standard surveys, and mean annual frequency (MAF) in standard surveys and other surveys, for non-passerine landbird species. Species order and abbreviations are as in Table 1.

Species	Standard surveys							Other surveys		
	Wi	Sp	Su	Au	MAF	Range	Years	MAF	Range	Years
Crested Pigeon	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.99	0.06	(5)
Australian Kestrel	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.85	0.17	(5)
Bar-shouldered Dove	1.00	0.80	1.00	1.00	0.95	0.25	(5)	0.98	0.06	(5)
Peaceful Dove	1.00	1.00	1.00	0.80	0.95	0.25	(5)	0.96	0.11	(5)
Pale-headed Rosella	1.00	1.00	0.80	1.00	0.95	0.25	(5)	0.93	0.29	(5)
Feral Pigeon	1.00	1.00	1.00	0.80	0.95	0.25	(5)	0.82	0.42	(5)
Spotted Turtle-Dove	0.80	0.80	1.00	0.80	0.85	0.25	(5)	0.81	0.35	(5)
Pheasant Coucal	0.80	0.80	1.00	0.80	0.85	0.50	(5)	0.66	0.34	(5)
Rainbow Bee-eater	0.80	0.80	0.60	1.00	0.80	0.75	(5)	0.81	0.41	(5)
Laughing Kookaburra	1.00	0.60	0.40	0.80	0.70	0.50	(5)	0.94	0.12	(5)
Scaly-breasted Lorikeet	0.80	0.60	0.40	0.40	0.55	0.50	(5)	0.67	0.36	(5)
Galah	0.40	0.80	0.60	0.20	0.50	0.50	(5)	0.49	0.24	(5)
Common Koel	-	0.80	1.00	-	0.45	0.25	(5)	0.30	0.24	(5)
Black-shouldered Kite	0.80	0.60	0.20	0.20	0.45	0.50	(5)	0.25	0.11	(5)
Sacred Kingfisher	0.20	0.80	0.60	-	0.40	0.25	(5)	0.51	0.18	(5)
Cockatiel	0.60	0.40	0.20	0.40	0.40	0.50	(5)	0.39	0.15	(5)
Wedge-tailed Eagle	0.80	0.20	-	0.60	0.40	0.50	(5)	0.26	0.23	(5)
Brown Falcon	0.40	0.20	0.20	0.40	0.30	0.25	(5)	0.27	0.34	(5)
Dollarbird	-	0.40	0.60	-	0.25	0.50	(4)	0.40	0.07	(5)
Brown Quail	-	0.40	0.40	0.20	0.25	0.75	(2)	0.15	0.44	(4)
Horsfield's Bronze-Cuckoo	-	0.60	0.40	-	0.25	0.50	(4)	0.11	0.17	(4)
Channel-billed Cuckoo	-	0.60	0.20	-	0.20	0.50	(3)	0.25	0.20	(5)
Brush Cuckoo	-	0.20	0.60	-	0.20	0.50	(3)	0.23	0.14	(5)
Brown Goshawk	0.40	0.20	-	0.20	0.20	0.50	(4)	0.09	0.12	(4)
Common Bronzewing	-	0.20	-	0.20	0.10	0.50	(1)	0.13	0.24	(4)
Azure Kingfisher	-	-	-	0.40	0.10	0.25	(2)	0.07	0.15	(3)
Pallid Cuckoo	-	0.40	-	-	0.10	0.25	(2)	0.04	0.18	(2)
Spotted Harrier	0.40	-	-	-	0.10	0.25	(2)	0.02	0.06	(2)
White-throated Needletail	-	-	0.40	-	0.10	0.25	(2)	0.02	0.06	(2)
Fan-tailed Cuckoo	-	0.20	-	-	0.05	0.25	(1)	0.26	0.19	(5)
Shining Bronze-Cuckoo	-	0.20	-	-	0.05	0.25	(1)	0.19	0.45	(4)
Stubble Quail	-	-	0.20	-	0.05	0.25	(1)	0.13	0.26	(3)
Rainbow Lorikeet	0.20	-	-	-	0.05	0.25	(1)	0.09	0.18	(4)
Australian Hobby	-	0.20	-	-	0.05	0.25	(1)	0.05	0.18	(3)
Peregrine Falcon	-	0.20	-	-	0.05	0.25	(1)	0.02	0.11	(1)
Grey Goshawk	-	-	0.20	-	0.05	0.25	(1)	0.01	0.05	(1)
Rose-crowned Fruit-Dove	-	-	0.20	-	0.05	0.25	(1)	-	-	
Forest Kingfisher	-	-	-	0.20	0.05	0.25	(1)	-	-	
Little Lorikeet	-	-	-	-	-	-		0.26	0.19	(5)
Whistling Kite	-	-	-	-	-	-		0.10	0.39	(4)
Blue-winged Kookaburra	-	-	-	-	-	-		0.07	0.22	(3)
Pacific Baza	-	-	-	-	-	-		0.06	0.11	(4)
Painted Button-quail	-	-	-	-	-	-		0.05	0.17	(2)
Emerald Dove	-	-	-	-	-	-		0.05	0.11	(3)
Collared Sparrowhawk	-	-	-	-	-	-		0.04	0.10	(3)
White-bellied Sea-Eagle	-	-	-	-	-	-		0.04	0.22	(1)
Marsh Harrier	-	-	-	-	-	-		0.04	0.17	(2)
Tawny Frogmouth	-	-	-	-	-	-		0.04	0.18	(2)
Australian Brush-turkey	-	-	-	-	-	-		0.03	0.06	(3)
Australian King-Parrot	-	-	-	-	-	-		0.03	0.11	(2)
Little Bronze-Cuckoo	-	-	-	-	-	-		0.03	0.06	(3)
Sulphur-crested Cockatoo	-	-	-	-	-	-		0.02	0.06	(2)
Musk Lorikeet	-	-	-	-	-	-		0.02	0.12	(1)
Crimson Rosella	-	-	-	-	-	-		0.02	0.08	(1)
Little Eagle	-	-	-	-	-	-		0.01	0.04	(1)
Topknot Pigeon	-	-	-	-	-	-		0.01	0.04	(1)
Brown Cuckoo-Dove	-	-	-	-	-	-		0.01	0.06	(1)
Wonga Pigeon	-	-	-	-	-	-		0.01	0.06	(1)
Southern Boobook	-	-	-	-	-	-		0.01	0.05	(1)
Barking Owl	-	-	-	-	-	-		0.01	0.05	(1)

species observed was 192. Tables 1, 2 & 3 separate observations for, respectively, waterbirds (44 species, 32 in standard surveys), non-passerine landbirds (60, 38) and passerines (88, 61). In each table species are ranked in descending order of MAF.

Seventy-seven species (41%, 30% and 47% of waterbirds, non-passerine landbirds and passerines, respectively) were observed every year in the standard surveys and 112 species (64%, 38% and 69%) in other surveys. Ninety-one species (55%, 35% and 52%) qualified as *principal* species.

Variation in Annual Frequency of Observation of Species

All species are classed according to variation in annual frequency in Table 4. In standard surveys, variation in frequency across years was low for 80 species (48 principal species). Variation was also low for 52 of these species (32 principal species) in the other surveys. In contrast, annual variation for Glossy Ibis, Yellow-billed Spoonbill, Hardhead, Black-winged Stilt, White-throated Gerygone, Zebra Finch and Pied Currawong was high in the other surveys. Seventeen species had high variation in annual frequency in standard surveys, but only Comb-crested Jacana and Common Myna were as variable in the other surveys. Most species that occurred only in the other surveys had low variation in annual frequency.

Variation in annual frequency among waterbirds, especially the shoreline species, was largely attributable to low frequencies in 1983-84.

In the standard surveys, annual frequencies of Pacific Heron decreased through the survey period ($P<0.05$) while those of Brown Quail increased ($P<0.05$). No consistent trends were detected across years for any other species observed in standard surveys. In other surveys, annual frequencies of eight species increased significantly through the survey period ($P<0.05$). However, the frequencies for Plumed Whistling-Duck, Grey Shrike-thrush, Weebill, White-throated Gerygone, Buff-rumped Thornbill, White-throated Honeyeater and Pied Currawong were also related to annual variation in the frequency of visits to eucalypt forest at Tallegalla, while that for Common Myna was related to frequency of visits to both Woolshed Creek Road and Prenzlau Swamp.

Because most species (131, 68%) showed little variation in frequency between years, and much of the variation for the remainder was correlated with the frequency of visits to specific habitats in different years, subsequent sections are concerned only with MAF and MSF values over the five years.

Mean Annual Frequency (MAF)

In standard surveys, 75% of waterbird and passerine species, but only 55% of non-passerine landbird species, were principal species (Tables 1-3). More of the waterbird (38%) and passerine species (39%) than of the non-passerine landbird species (21%) were among the birds observed most regularly, i.e. in over 80% of surveys.

In the other surveys, 57, 40 and 64% of waterbird, non-passerine landbird and passerine species, respectively, were observed in over 20% of surveys; 16 to 20% of the species in these three categories were observed in over 80% of surveys.

For most species, MAF was similar in standard and other surveys. All species with high MAF (>0.8) in standard surveys had an MAF of at least 0.5 in other surveys. Among species with intermediate MAF (0.21 to 0.80) in standard surveys, MAF in other surveys for Laughing Kookaburra, Grey Shrike-thrush, Speckled Warbler and Varied Triller was substantially greater (>0.2 units) and that for Royal Spoonbill, Black-fronted Plover, Fairy Martin, Richard's Pipit, Red-backed Fairy-wren, Chestnut-breasted Mannikin, Tawny Grassbird and Singing Bushlark was substantially lower. Fan-tailed Cuckoo, Leaden Flycatcher, White-throated Gerygone and Pied Currawong, with low MAF (0.1 or less) in standard surveys, had MAF substantially greater in other surveys. Little Lorikeet and seven passerines that were absent from standard surveys had intermediate MAF in other surveys.

No specific family, or guild, of waterbirds was consistently observed at either high or low MAF. Among non-passerine landbirds, ground feeding pigeons and doves, including two introduced species, had high MAF, contrasting with fruit-doves which were seldom observed. Several raptors also had low MAF, but in contrast the Australian Kestrel was always observed. Among passerines, several small species (e.g. Superb Fairy-wren, Yellow Thornbill and White-browed Scrubwren) had high MAF as did the much larger, and conspicuous, Australian Magpie and Torresian Crow.

Mean Seasonal Frequency (MSF)

Twenty-six species were observed in standard surveys in all seasons of all years and another 27

TABLE 3. Mean seasonal frequency (MSF) in standard surveys, and mean annual frequency (MAF) in standard surveys and other surveys, for passerine species. Species order and abbreviations are as in Table 1.

Species	Standard surveys							Other surveys		
	Wi	Sp	Su	Au	MAF	Range	Years	MAF	Range	Years
Willie Wagtail	1.00	1.00	1.00	1.00	1.00	0.00	(5)	1.00	0.00	(5)
Australian Magpie-lark	1.00	1.00	1.00	1.00	1.00	0.00	(5)	1.00	0.00	(5)
Australian Magpie	1.00	1.00	1.00	1.00	1.00	0.00	(5)	1.00	0.00	(5)
Torresian Crow	1.00	1.00	1.00	1.00	1.00	0.00	(5)	1.00	0.00	(5)
Superb Fairy-wren	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.99	0.06	(5)
Striped Honeyeater	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.99	0.05	(5)
Noisy Miner	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.97	0.06	(5)
Black-faced Cuckoo-shrike	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.96	0.12	(5)
Silvereye	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.96	0.10	(5)
Lewin's Honeyeater	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.95	0.12	(5)
Double-barred Finch	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.95	0.11	(5)
Pied Butcherbird	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.95	0.15	(5)
Common Starling	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.94	0.21	(5)
Figbird	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.85	0.24	(5)
Welcome Swallow	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.78	0.38	(5)
Golden-headed Cisticola	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.78	0.30	(5)
Zebra Finch	1.00	1.00	1.00	1.00	1.00	0.00	(5)	0.74	0.53	(5)
Grey Butcherbird	0.60	1.00	1.00	1.00	0.90	0.25	(5)	0.86	0.41	(5)
Yellow-rumped Thornbill	0.80	0.80	1.00	1.00	0.90	0.25	(5)	0.57	0.23	(5)
Yellow Thornbill	1.00	0.60	1.00	0.80	0.85	0.25	(5)	0.93	0.06	(5)
Rufous Whistler	0.80	1.00	0.80	0.80	0.85	0.50	(5)	0.91	0.29	(5)
White-browed Scrubwren	1.00	0.80	0.60	1.00	0.85	0.50	(5)	0.75	0.13	(5)
Clamorous Reed-Warbler	0.60	1.00	1.00	0.80	0.85	0.50	(5)	0.69	0.31	(5)
House Sparrow	0.80	0.80	1.00	0.80	0.85	0.50	(5)	0.63	0.17	(5)
Grey-crowned Babbler	0.80	0.60	0.80	1.00	0.80	0.25	(5)	0.68	0.22	(5)
Fairy Martin	0.80	1.00	1.00	0.40	0.80	0.50	(5)	0.55	0.30	(5)
Eastern Whipbird	1.00	0.80	0.60	0.60	0.75	0.50	(5)	0.70	0.48	(5)
Brown Honeyeater	1.00	1.00	0.60	0.40	0.75	0.50	(5)	0.66	0.22	(5)
Richard's Pipit	1.00	0.60	0.80	0.60	0.75	0.50	(5)	0.34	0.32	(5)
Red-backed Fairy-wren	0.80	1.00	0.60	0.60	0.75	0.75	(5)	0.34	0.29	(5)
Striated Pardalote	1.00	0.80	-	0.80	0.65	0.25	(5)	0.80	0.35	(5)
Olive-backed Oriole	0.40	0.80	0.80	0.40	0.60	0.75	(5)	0.50	0.20	(5)
Rufous Fantail	-	1.00	0.80	0.40	0.55	0.50	(5)	0.55	0.25	(5)
Grey Shrike-thrush	0.20	0.60	0.40	0.80	0.50	1.00	(5)	0.83	0.29	(5)
White-backed Swallow	0.40	0.80	0.20	0.60	0.50	0.75	(4)	0.64	0.36	(5)
Eastern Yellow Robin	0.60	0.40	0.40	0.60	0.50	0.50	(5)	0.47	0.30	(5)
Speckled Warbler	0.40	0.20	0.60	0.60	0.45	0.75	(5)	0.74	0.32	(5)
Mistletoebird	0.20	0.60	0.60	0.40	0.45	0.50	(5)	0.58	0.47	(5)
Grey Fantail	1.00	-	-	0.80	0.45	0.25	(5)	0.47	0.15	(5)
Chestnut-breasted Mannikin	0.20	0.40	0.80	0.40	0.45	0.75	(4)	0.23	0.25	(5)
Tawny Grassbird	-	0.40	1.00	0.40	0.45	0.50	(5)	0.12	0.24	(4)
Varied Triller	0.20	0.40	0.20	0.40	0.30	0.50	(3)	0.61	0.60	(5)
Common Myna	0.20	0.20	0.40	0.40	0.30	0.75	(3)	0.37	0.68	(5)
Singing Bushlark	-	-	0.80	0.40	0.30	0.25	(5)	0.08	0.24	(4)
Golden Whistler	0.80	-	-	0.20	0.25	0.00	(5)	0.37	0.20	(5)
Variegated Fairy-wren	0.40	0.60	-	-	0.25	0.50	(3)	0.32	0.41	(5)
White-winged Triller	-	0.60	0.20	-	0.20	0.25	(4)	0.08	0.15	(3)
Black-faced Monarch	-	0.20	0.20	0.20	0.15	0.50	(2)	0.13	0.26	(4)
Tree Martin	-	-	0.40	0.20	0.15	0.50	(2)	0.07	0.28	(2)
Pied Currawong	0.40	-	-	-	0.10	0.25	(2)	0.50	0.71	(5)
Spangled Drongo	0.20	-	-	0.20	0.10	0.25	(2)	0.29	0.34	(5)
Restless Flycatcher	0.20	0.20	-	-	0.10	0.25	(2)	0.12	0.41	(3)
Nutmeg Mannikin	0.20	-	-	0.20	0.10	0.50	(1)	0.11	0.24	(3)
Eastern Spinebill	0.20	-	-	0.20	0.10	0.25	(2)	0.10	0.24	(4)
White-throated Gerygone	-	0.20	-	-	0.05	0.25	(1)	0.69	0.60	(5)
Leaden Flycatcher	-	0.20	-	-	0.05	0.25	(1)	0.32	0.37	(5)
Yellow-faced Honeyeater	-	-	-	0.20	0.05	0.25	(1)	0.21	0.18	(5)
Little Friarbird	-	0.20	-	-	0.05	0.25	(1)	0.20	0.37	(5)
Red-browed Firetail	-	0.20	-	-	0.05	0.25	(1)	0.17	0.21	(5)
Rose Robin	-	-	-	0.20	0.05	0.25	(1)	0.12	0.17	(5)
Little Cuckoo-shrike	0.20	-	-	-	0.05	0.25	(1)	0.01	0.06	(1)
White-throated Honeyeater	-	-	-	-	-	-		0.66	0.76	(5)
Buff-rumped Thornbill	-	-	-	-	-	-		0.47	0.83	(5)

TABLE 3. Cont. Species order and abbreviations are as in Table 1.

Species	Standard surveys							Other surveys		
	Wi	Sp	Su	Au	MAF	Range	Years	MAF	Range	Years
Weebill	-	-	-	-	-	-		0.44	0.65	(5)
Scarlet Honeyeater	-	-	-	-	-	-		0.41	0.30	(5)
White-throated Treecreeper	-	-	-	-	-	-		0.39	0.49	(5)
Varied Sittella	-	-	-	-	-	-		0.30	0.43	(5)
Spotted Pardalote	-	-	-	-	-	-		0.23	0.23	(5)
Cicadabird	-	-	-	-	-	-		0.18	0.14	(5)
Jacky Winter	-	-	-	-	-	-		0.18	0.25	(5)
Noisy Friarbird	-	-	-	-	-	-		0.12	0.28	(4)
White-breasted Woodswallow	-	-	-	-	-	-		0.06	0.11	(3)
Rufous Songlark	-	-	-	-	-	-		0.05	0.18	(2)
Ground Cuckoo-shrike	-	-	-	-	-	-		0.03	0.12	(1)
Little Shrike-thrush	-	-	-	-	-	-		0.02	0.06	(2)
Dusky Woodswallow	-	-	-	-	-	-		0.02	0.10	(1)
Regent Bowerbird	-	-	-	-	-	-		0.02	0.12	(1)
Yellow-eyed Cuckoo-shrike	-	-	-	-	-	-		0.01	0.06	(1)
Scarlet Robin	-	-	-	-	-	-		0.01	0.04	(1)
Crested Shrike-tit	-	-	-	-	-	-		0.01	0.05	(1)
Satin Flycatcher	-	-	-	-	-	-		0.01	0.04	(1)
Little Grassbird	-	-	-	-	-	-		0.01	0.06	(1)
Brown Songlark	-	-	-	-	-	-		0.01	0.06	(1)
Brown Gerygone	-	-	-	-	-	-		0.01	0.06	(1)
Blue-faced Honeyeater	-	-	-	-	-	-		0.01	0.06	(1)
Fuscous Honeyeater	-	-	-	-	-	-		0.01	0.06	(1)
Plum-headed Finch	-	-	-	-	-	-		0.01	0.06	(1)
Satin Bowerbird	-	-	-	-	-	-		0.01	0.04	(1)

in all seasons of at least three years (i.e. MSF of 0.6 or higher). MSF values for another 25 species observed in standard surveys varied from lows of 0.0 or 0.2 to highs of 0.6 or 0.8, respectively, or higher; for eight of them minimum MSF on other surveys were always intermediate (>0.2) and, thus, only 17 species showed clear differences in seasonal presence. Another 11 species that were either missing from standard surveys, or observed at low MAF (0.2 or less) on those surveys, had minimum MSF<0.2 and a range >0.3 in other surveys, indicating that they also differed in seasonal presence. MSF in other surveys for Darter (range 0.0 to 0.28) and Black- faced Monarch (0.0 to 0.22) were consistent with those in standard surveys, confirming the small differences in seasonal presence. Approximate dates on which these 30 species with clear differences in MSF were present are shown in Fig. 2.

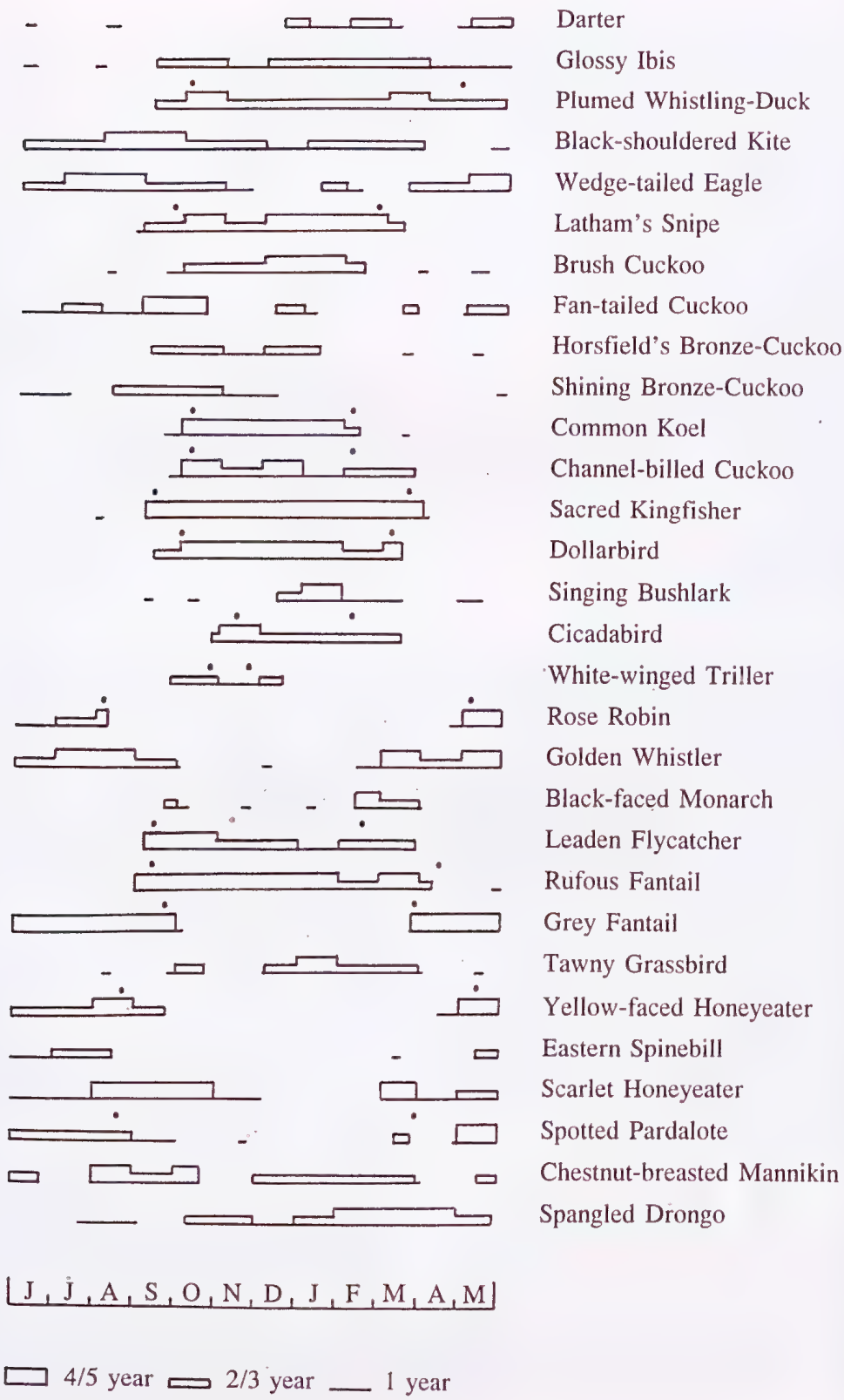
DISCUSSION

The Value of Information on Frequency of Observation

Knowledge of ways in which abundance of bird species is influenced by land use is essential to wildlife management. For a limited range of habitats, e.g. commercial forests, this can be readily obtained in structured, systematic surveys. Such surveys have not been done over farming landscapes, and management decisions depend substantially on opportunistic information.

The standard survey adequately monitored changes in abundance of individual species within seasons, but inferences on the relative abundance of different species, and of individual species between seasons, need to take account of differences in detectability (Emlen, 1971; Davies, 1984; Recher, 1988). Estimates of abundance also need to be based on several years of survey (Rice et al., 1983). The variable climate in Australia, particularly in southeast Queensland, makes this even more important. However, variation in frequency between years for most species in the Marburg district was low. The major exceptions were waterbirds that move nomadically in response to inland rainfall (Gosper et al., 1983; Woodall, 1985), and it is generally more useful to relate their frequency of occurrence to proximate causal factors than to determine unadjusted long-term mean frequencies. The wide variation in annual frequency for some land birds was associated with proportion of visits to a eucalypt association, reflecting restricted use of habitat in the district and the limitations of the other surveys.

Notwithstanding the preceding comments, the combination of seasonally balanced standard surveys with a larger number of other surveys pro-


Darter
Glossy Ibis
Plumed Whistling-Duck
Black-shouldered Kite
Wedge-tailed Eagle
Latham's Snipe
Brush Cuckoo
Fan-tailed Cuckoo
Horsfield's Bronze-Cuckoo
Shining Bronze-Cuckoo
Common Koel
Channel-billed Cuckoo
Sacred Kingfisher
Dollarbird
Singing Bushlark
Cicadabird
White-winged Triller
Rose Robin
Golden Whistler
Black-faced Monarch
Leaden Flycatcher
Rufous Fantail
Grey Fantail
Tawny Grassbird
Yellow-faced Honeyeater
Eastern Spinebill
Scarlet Honeyeater
Spotted Pardalote
Chestnut-breasted Mannikin
Spangled Drongo
J J A S O N D J F M A M
4/5 year
2/3 year
1 year

vides adequate baseline information on seasonal and annual frequency of species for habitat management. The standard surveys are repeatable, and continue, enabling long-term changes to be monitored and compared with similar information from elsewhere (e.g. the Australian Bird Count; Ambrose, 1989). Although it would be impracticable to precisely repeat the other surveys, their number and broadly specified representation of habitats ensures a useful baseline to which changes can be related.

Frequency of Observation of Species

Waterbirds. Most of the principal waterbirds observed in the Marburg district (Table 1) are widely distributed in Australia, with 17 species occurring in over 40% of 1°grid squares (Blakers et al., 1984). Those with more restricted distribution include Cattle Egret, Intermediate Egret, Plumed Whistling-Duck, Dusky Moorhen, Purple Swamphen and Latham's Snipe. In contrast, some widespread species such as Australian Pelican, Great Cormorant and Pied Cormorant were seldom observed, even though their relative frequencies were greater than 60% in annual one-day counts for the region within 80km of Brisbane between 1972 and 1983 (Woodall, 1985). Twenty principal species were also common in northeast NSW. (Gosper, 1981; Gosper et al., 1983), with the Maned Duck the conspicuous exception.

The Marburg district, like the whole of southeast Queensland (Woodall, 1985) and northeast NSW. (Gosper, 1981; Gosper et al., 1983) is clearly rich in waterbirds. It supports many more species than regions inland of the Great Divide (Whitmore et al., 1983; Crossman & Reimer, 1986). Rural residential settlement has increased the number of dams to about 3 per km^2(see Queensland Dept Mapping and Survey, Marburg Topographic Map 9442-44). Although many dams are small and lack habitat diversity (G.J. Leach, unpublished data), they supplement older, and usually larger, dams and ephemeral shallow swamps which provide more diverse habitat (Braithwaite, 1975; Leach & Hines, 1992; Wilkinson and Schwenke, 1992). Absence of major reservoirs probably restricts deep water feeders such as Australian Pelican and the large cormorants.

The range in annual frequency was generally wider for waterbird species than for landbirds with the same MAF. Lower frequency of shoreline species in 1983-84 coincided with the end of a widespread southeast Australian drought, enabling them and birds of open water, e.g. cormorants and most ducks, to disperse inland, west of the Great Divide (Woodall, 1985; Leach & Hines, 1992). In contrast higher annual frequencies for several species occurred in the drier 1980-81 and 1982-83 years.

Non-passerine landbirds. Eleven of the principal non-passerine landbirds (Table 2) are widely distributed in Australia and the remaining 10 species occur in at least 11% of 1°grid squares (Blakers et al., 1984). Among the most frequently observed, Spotted Turtle-Dove, Peaceful Dove and Cockatiel were better represented at Marburg than in surrounding districts.

The principal species are birds of open country, the 'edge' between woody vegetation and open country, or farmlands. Few were numerous and five with a MAF of 0.5 or higher were ground-feeding pigeons and three were parrots. The Feral Pigeon, Spotted Turtle-Dove, Crested Pigeon and Galah were commensal with farming, and their abundance probably reflects the intensity of small-scale cropping, whereas the Peaceful Dove and Bar-shouldered Dove appear to depend on softwood scrub remnants. Among remaining species with MAF of 0.5 or higher, Australian Kestrel and Rainbow Bee-eater hunt over open country and contrast with Scaly-breasted Lorikeet, Pale-headed Rosella and Laughing Kookaburra utilising open-forest/woodland and the Pheasant Coucal using dense scrub and/or rank grass. Sacred Kingfisher was the only species with MAF>0.5 in other surveys that had MAF<0.5 in standard surveys, probably reflecting its preference for the open eucalypt forest with many termitaria for nest sites.

The most notable feature of the non-passerine landbirds was that half of them were observed on 5% or fewer visits, yet none are rare in southeast Queensland (Roberts, 1979). They included several raptors and parrots. The group also included the fruit-doves usually associated with closed-forest or softwood scrub, even though the district has many, isolated, *Ficus* spp. which produce heavy crops of fruit (Leach & Hines, 1987). The remnants of low closed-forest may be too small, too degraded, too isolated from extensive rainfor-

FIG. 2. Periods when species with substantial differences in MSF (see text) were present. Continuous lines/blocks join observations at closer than 4-week intervals, based on combined observations over 5 years. Number of years when species were present in each month and single observations are shown. Mean dates of arrival and departure of strongly seasonal migrants are also shown (●).

TABLE 4. The numbers of principal and non-principal species in standard surveys, and of species observed only in other surveys, classed according to low, medium and high variation in annual frequency. For standard surveys low, medium and high variation are represented by values of 0.0 or 0.25, 0.5, and 0.75 or 1.0 respectively; for other surveys the corresponding values are <=0.25, 0.26 to 0.5, and >0.5 respectively. The numbers of species with MAF <=0.20 in other surveys are shown in parentheses.

Range in annual frequency		Water-birds	Non-Passerines landbirds	Passerines	Total
Standard surveys	Other surveys				
Principal species					
Low	Low	6	6	20 (1)	32 (1)
"	Medium	5	4	4	13
"	High	2	0	1	3
Medium	Low	1	7 (1)	5 (1)	13 (2)
"	Medium	1	2	7	10
"	High	2	0	2	4
High	Low	0	0	2	2
"	Medium	6	2 (1)	4	12 (1)
"	High	1	0	1	2
Sub-total		24	21 (2)	46 (2)	91 (4)
Non-principal species					
Low	Low	3 (3)	11 (10)	6 (5)	20 (18)
"	Medium	0	4 (2)	4 (2)	8 (4)
"	High	2 (1)	0	2	4 (1)
Medium	Low	2 (2)	2 (2)	1 (1)	5 (5)
"	Medium	0	0	2 (2)	2 (2)
"	High	0	0	0	0
High	Low	0	0	0	0
"	Medium	1 (1)	0	0	1 (1)
"	High	0	0	0	0
Sub-total		8 (7)	17 (14)	15 (10)	40 (31)
Species observed on only the other surveys					
—	Low	10 (10)	21 (20)	20 (19)	51 (49)
—	Medium	1 (1)	1 (1)	4 (1)	6 (3)
—	High	1 (1)	0	3	4 (1)
Sub-total		12 (12)	22 (21)	27 (20)	61 (53)
Total		44 (19)	60 (37)	88 (32)	192 (88)

est and/or naturally floristically unsuitable for other than limited opportunistic exploitation by fruit-doves. Fruit-doves were only occasionally observed immediately following European settlement at Murphy's Creek, 50km west (Lord, 1956), but whether they were more prominent in the more extensive softwood scrub of the Marburg District (Elsol, 1991) cannot be ascertained.

Passerines. Twenty-three principal passerines (Table 3) have a wide Australian distribution, while five were reported from <11% of 1°grid squares (Blakers et al., 1984). The latter include species associated with closed-forest (Varied Triller, Eastern Whipbird and Lewin's Honeyeater) or rank grassland (Tawny Grassbird) and the Common Myna. Nine species with low MAF (0.2 or less) (Tree Martin, White-winged Triller, Jacky Winter, Restless Flycatcher, Rufous Songlark, Brown Songlark, Weebill, Varied Sittella and White-breasted Woodswallow) are widely distributed in Australia. Nine non-principal species are restricted to <11% of the Australian 1° grid squares, with Yellow-eyed Cuckoo-shrike, Black-faced Monarch, Little Cuckoo-shrike, Brown Gerygone, Satin Bowerbird and Regent Bowerbird associated with closed-forest. Species observed more frequently than in neighbouring grid squares include Grey-

crowned Babbler, Superb Fairy-wren, Yellow Thornbill, Speckled Warbler, Striped Honeyeater and Zebra Finch.

Passerines are clearly the most important component of the avifauna, both in terms of species number (Leach & Hines, 1987) and frequency of observation (Table 3). Thirty-three of the species listed in Table 3 were observed in roadside remnant vegetation in summer, including 31 principal species (Leach & Recher, 1993). The six most numerous species in roadside remnants, namely Silvereye, Superb Fairy-wren, Yellow Thornbill, Double-barred Finch, Red-backed Fairy-wren and Lewin's Honeyeater had MAF of 0.75 or more.

Cicadabird, Weebill, White-throated Gerygone, Buff-rumped Thornbill, Varied Sittella, White-throated Treecreeper, White-throated Honeyeater and Spotted Pardalote, with much higher MAF in other surveys than in standard surveys, are largely restricted to the eucalypt associations (G.J. Leach, unpublished data), corroborated by correlation of their MAF with proportion of visits to eucalypt stands at Tallegalla. Other differences in MAF between surveys also reflect the proportion of visits to eucalypt associations, e.g. Yellow-faced Honeyeater and Pied Currawong.

Among species with greater MAF in standard surveys than in other surveys, the narrow range in annual frequencies for Singing Bushlark, Tawny Grassbird and Yellow-rumped Thornbill confirms their localised distribution. This reflects preference for open country, rank grassland, and close-grazed or mown grassland around isolated trees, respectively (Leach & Hines, 1987). Larger ranges in annual frequency contribute to the difference in MAF between surveys for Fairy Martin, Richard's Pipit and Red-backed Fairy-wren, but at least part of the difference for the first two is likely to reflect preference for open habitat. The difference for the Red-backed Fairy-wren may be related to its abundance in roadside vegetation (Leach & Recher, 1993) and use of swamp grasslands (Leach & Hines, 1987).

The introduced Common Myna colonized the district from the west during this survey, reaching the eastern boundary in 1982 (Leach & Hines, 1987). Correlations with visits to Woolshed Creek Road and Prenzlau, in the west, probably reflect marginally longer colonization in these areas.

A wide range of families and feeding strategies are represented among principal passerines. Approximately half the species primarily use open, or disturbed, habitats (Schodde & Tidemann, 1986). Exceptions associated with closed-forest/softwood scrub include Varied Triller, Grey Shrike-thrush, Rufous Fantail, Eastern Whipbird, White-browed Scrubwren, Yellow Thornbill, Silvereye, Lewin's Honeyeater and Figbird (Howe, 1986; Leach & Recher, 1993).

Species using rainforest patches in northern NSW were grouped according to size of patch occupied (Howe, 1986). The first 21 species listed in Table 3 were not in the more specialised rainforest groups. The Rufous Fantail and White-throated Treecreeper were placed in a group requiring patches larger than 2.5 ha. However, the Rufous Fantail was common in narrow roadside remnants at Marburg (Leach & Recher, 1993), whereas the White-throated Treecreeper was mainly observed in open eucalypt forest on other surveys. Several species occurring in small and large rainforest patches, but predominantly the latter, were observed in roadside remnants at Marburg, indicating that habitat use differs from that in northern NSW. An explanation for the differences may be that abundant Lantana (*Lantana camara*) and other woody weeds provide a more effective linkage between small remnant patches for many bird species than in northern NSW (Lynch, 1987; Lynch & Saunders, 1991; McIntyre & Barrett, 1992; Leach & Recher, 1993). Because the diversity and abundance of passerines may be more vulnerable to intensified land use than their current status indicates (cf. Recher & Lim, 1990), it may become especially important to retain, and where possible regenerate, native woody vegetation if woody weeds are substantially controlled and cleared.

Seasonal Migrants

Surveys were sufficiently frequent to provide approximate dates of arrival and departure of migrant species (Fig 2). Some species are clearly summer (e.g. Latham's Snipe, Common Koel, Leaden Flycatcher and Rufous Fantail) or winter (e.g. Rose Robin, Grey Fantail and Yellow-faced Honeyeater) visitors, with little variation between years in dates of first or last observation. Some tended to be absent from the district for only a very short period (e.g. Black-shouldered Kite and Wedge-tailed Eagle) while White-winged Triller was present for only a short period. Others (e.g. Scarlet Honeyeater and Spotted Pardalote) were consistently observed at disjunct intervals. Several migrants consistently arrived in late September, e.g Common Koel and Dollarbird, but dates of last observation were more variable.

Information for southeast Queensland, mainly limited to honeyeaters at Wellington Point (Robertson, 1958, 1965; Robertson & Woodall, 1983), is significantly augmented. Features of special interest are the small period of overlap between the Rufous Fantail and the Grey Fantail in September and March/early April, the short winter presence of the Rose Robin, the short visit of the White-winged Triller for breeding (G.J. Leach, unpublished data), and migration patterns in the honeyeaters. Low MSF in summer and/or autumn for some otherwise relatively common raptors indicates that further study is necessary to establish if this is the result of seasonal movement, or is associated with behavioural changes that affect detectability while breeding. Latham's Snipe is the only truly seasonal migrant among the principal waterbirds because Plumed Whistling-Duck is a winter resident in the neighbouring grid square (Leach & Hines, 1987). Information for other waterbirds, e.g. Black Swan and Glossy Ibis, reflects nomadic movements.

Summer presence of the Rufous Fantail in the Marburg district agrees with observations in northeast NSW. (Cameron, 1985). However, the Grey Fantail was more numerous in summer than winter in NSW. Roberts (1979) remarks that Grey Fantails are resident in southeast Queensland with an increase in numbers in winter. Our data shows that it is not resident in all habitats, possibly because different races may occupy different habitats (Cameron, 1985). Mist netting since 1988 has shown that small numbers of both species are present outside the dates in Fig. 2 (G. R. Anderson & G.J. Leach, unpublished data), suggesting that more monitoring of their movements is necessary.

Observations for the Yellow-faced Honeyeater and Eastern Spinebill (Fig. 2) closely match those of Robertson and Woodall (1983). The continuous presence of Scarlet Honeyeaters at Wellington Point from March through September contrasts with its frequent absence through midwinter in the Marburg district where it, and also the Spotted Pardalote, appear to be seasonal migrants responding to local variation in availability of food.

CONCLUSIONS

The Marburg district supports a rich diversity of bird species, with waterbirds and passerines generally better represented than non-passerine landbirds. The diversity is sustained by the wetlands, remnants of brigalow softwood scrub, eucalypt open-forest and the woody weeds interspersed through the farmlands. The survey has established a robust database which will allow changes in mean annual and seasonal frequency of bird species to be detected. The information should be used to guide management of these diverse habitats.

While the avifauna (with the exception of most non-passerine landbirds) is well-adapted to the existing matrix of terrestrial and wetland habitats, additional human settlement and intensification of land use may lead to a breakdown of this matrix. Regular monitoring is vital. Maintenance of the present diversity and abundance of birds will require management strategies aimed at retention and better management of existing native woody vegetation, and re-vegetation with appropriate native species wherever practicable.

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APPENDIX 1 Details of localities in the standard survey which were surveyed on foot.

Location	Grid Ref.	Duration (mins)	Habitats			
			Roadside	Paddocks	Dams	Other
Haigslea (School)	MQ631500	45	T(1,A,B), G(s-r).	T(1,A), G(s), C(1).	M1, M2 & M3 (s) + 1(s, silted with *Typha* sp. and adjacent *Schinus terebinthifolia*).	School and church grounds. T(2, native & exotic), G(s).
Haigslea	MQ618495	20	G(r).	T(1,A), G(r), C(1).	M4(m) + 1(m).	
MT Marrow	MQ627481	20	T(2,S,A), W(2,L), G(r).	T(2,S,A), W(2,L), G(s-r).	M5(s).	Road metal quarry south of road.
Malabar	MQ609483	15	T(1,A), W(1,C,L), G(r).	T(1,A,B), W(1,L,C), G(m-r).	M6(1).	
Malabar	MQ609477	30	T(2,S,A,B), W(2,L) G(r).	T(1,S,A), W(1,L), G(m-s).		Dis-used sand quarry south of road. Cliffs used by hole-nesting species (see Leach and Hines, 1987).
Tallegalla (Railway dam)	MQ577467	10	T(1,A), W(1,C,L), G(m-r).	T(1,A,B), W(1,L), G(s).	1(m, covered with Water hyacinth, *Eichhornia crassipes*).	
Tallegalla (The Bluff)	MQ550464	30	T(2,S,A), W(2,L), G(m-r).	T(2,S,A), W(2,L), G(s-m).	2(s, often empty)	Three large *Ficus* spp. at this site.
Ashwell	MQ561446	20	T(2,S,A,B), W(2,L), G(r).	T(S,B,E,A), W(2,L), G(s-r).		Small creek through site
Minden Dam	MQ548522	15	T(1,A,S), G(s-r).	T(2,E,B,S), G(s-r).	1(m - Leach & Hines, 1992).	Mid-afternoon.

1. Grid References for Marburg (9442-44) and Haigslea (9442-41) 1:25 000 Topographic Maps.
2. Vegetation:
T - trees; 2, 1 - more than 5, and 1 to 5, respectively >8m tall in vicinity. Principal trees are Brigalow (*Acacia harpophylla*) (B), other acacia spp. (A), softwood species (S, see Leach & Hines, 1987), and eucalypts (E).
W - woody weeds; 2 - extensive thickets, 1 - isolated clumps; species include lantana (*Lantana camara*) (L) and Wait-a-while (*Caesalpinia decapetala*) (C).
G - grass; s - grazed short, m - medium grazed to about 500mm tall, r - rank, often not grazed and over 1000mm tall.
C - cultivated land nearby, <20% of total area within 500m of road.
Additional details of roadside vegetation on parts of the standard route are in Leach & Recher (1993).
3. Dams - those prefixed 'M' are described in Leach (1994). Minden is described in Leach & Hines (1992).
Dams are described as large (l, >15 000m^2 maximum surface area), medium (m, 5000 to 15 000m^2) or small (s, <5000m^2).

APPENDIX 2 Principal areas visited in the 100 non-standard surveys.

Locality	Number of visits	Habitats	Remarks
Haigslea/Malabar/ MT Marrow.	92[1]	As first five sites on standard route, plus extra softwood remnants.	82 to 100% of visits each year.
Schumans Road.	71[2]	Well-conserved lengths of softwood scrub gallery, about 7m wide (Leach & Recher, 1993).	24% of visits in 1980-81; 68 to 100% thereafter.
The Bluff, Tallegalla	19	See App.1.	10 to 29% of visits each year.
Woolshed Creek Road - East.	83[2]	Lengths of softwood scrub gallery, about 8m wide plus small creek and gallery of *Melaleuca bracteata*.	65% of visits in 1980-81, progressively increasing to 100% in 1984-85.
Woolshed Creek Road - West.	78[2]	Eucalptus open-forest (especially *E. maculata*) with woody weeds and grazed grass understorey (Leach & Hines, 1987).	47% of visits in 1980-81, increasing through 69, 84, 90 and 100% in following years.
Glamorgan Vale - MT Stradbroke.	9	As Haigslea/Malabar/MT Marrow, plus more extensive areas of relatively intact Brigalow-softwood scrub.	29% of visits in 1980-81, 15% in 1981-82, none subsequently.
Prenzlau Swamp[3].	36	Shallow ephemeral swamp (Leach & Hines, 1987).	First visited in March 1981; 18% of visits in 1980-81, increasing through 23, 32, 40 and 72% in following years.

(1) Censuses of farm dams (Dams M1 to M6, see Appendix 1) were major objectives on 14 of these visits.
(2) Transect censuses carried out on 12 of these days and rolling bird surveys (Cullen, 1980) on another 40 days. Five rolling bird surveys were completed in spring and autumn of each of the last four years, substantially contributing to the discrepancy in number of visits between seasons.
(3) Prenzlau Swamp. Extensive open water (c.100ha) in March 1981, reduced by 80% by October 1981 and almost no open water by October 1982. Flooded in May 1983 and extensive open water thereafter apart from early summer 1984-85.

CRAB ISLAND REVISITED : REASSESSMENT OF THE WORLD'S LARGEST FLATBACK TURTLE ROOKERY AFTER TWELVE YEARS

COLIN J. LIMPUS, P. J. COUPER AND K. L. D. COUPER

Limpus, C.J., Couper, P.J. & Couper, K.L.D. 1993 06 30 : Crab Island revisited: reassessment of the world's largest Flatback Turtle rookery after twelve years. *Memoirs of the Queensland Museum* 33(1):277-289. Brisbane. ISSN 0079-8835.

Crab Island in northeastern Gulf of Carpentaria supports the largest nesting population of *Natator depressus*, a marine turtle endemic to the Australian continental shelf, and low density nesting by *Eretmochelys imbricata*. The reproductive status of the Flatback Turtle, *Natator depressus*, at Crab Island, is reassessed after 12 years based on a survey conducted during high density nesting in July 1991. *N. depressus* hatchling productivity from the island continues to be high. The characteristic small size of nesting females and egg diameters of *N. depressus* that breed in the Crab Island region suggests that this population is a different breeding unit from that of the southern Great Barrier Reef. The feeding areas supplying turtles to the Crab Island region rookeries extend as far north as southern Irian Jaya.
☐ *Natator depressus, Eretmochelys imbricata, Crab Island, Queensland, Australia, nesting, hatchling productivity, conservation status.*

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Crab Island, in the north eastern Gulf of Carpentaria, supports the largest recorded nesting aggregation of Flatback Turtles, *Natator depressus* (Limpus & Parmenter, 1986). *N. depressus* is almost totally confined to the Australian continental shelf and its breeding is restricted to Australia (Limpus et al. 1988). The biology of marine turtle populations breeding on Crab Island was reviewed by Limpus et al. (1983a) based on field surveys of the nesting turtles in 1970-1979. Because the status of this significant turtle breeding population had not been reassessed since that time, a study to redescribe the reproductive biology of the Crab Island turtles after a 12 year interval was undertaken in July 1991, during the high density nesting period identified in previous studies (Limpus et al. 1983a).

METHODS

A two person team camped on Crab Island during 6-22 July 1991 (P.J.C. and K.L.D.C.). The western (ocean) beach of the island was measured along the spring high tide level and subdivided into eleven numbered sectors (each 500m long) from south to north (Fig. 1) using a pedometer. All data recorded along the island were scored by beach sector. The beach width within sectors 1-10 was measured from the spring high tide level to the crest of the seaward dune adjacent at each sector mark. These were the sectors in which all turtle nesting activity occurred. On arrival, the team counted all existing turtle tracks by species, without attempting to age the tracks. A single track included both the emergence and return crawl of a nesting turtle. All tracks were crossed off in the sand above the high tide mark as they were counted so that previously recorded tracks could be recognised. Thereafter, a track census was conducted daily: all turtle tracks and nests from which hatchlings had emerged from the previous night were counted by species along the western beach. Because two persons could not monitor the nesting behaviour of all turtles ashore for a night along 6km of beach, a subset of the beach sectors (4 to 6) was selected for nightly measurement of nesting success of each turtle. Potential predators of the turtles, their eggs or hatchlings were identified and quantified where possible. This included counting of crocodile and bird tracks. Turtles were recorded in the waters adjacent to the nesting beach during the daily census of tracks on those days when the weather was relatively calm. As well, a male turtle was captured by 'beach jumping' (cf. Limpus & Reed, 1985).

Opportunistic tagging of nesting female turtles occurred when volunteer members of the Queensland Turtle Research Project visited Crab Island (28 December 1989 and 15-17 January, 1991) and the south beach at the mouth of the Jardine River on the mainland, 14km from Crab Island (29 December 1987). Adult turtles were tagged using

serially numbered, self piercing, self locking tags applied to the axillary flipper tagging position (Limpus & Reed, 1985). In July 1991, 3.3g monel tags (National Band and Tag Company, style 1005, size 681; SD = 0.01g, range = 3.25-3.29, n = 50), inscribed with a return address on the reverse side (Ecology, Box 26 Woden 2606 Australia), were used. On the other visits, 4.1g titanium turtle tags (Stockbrands Co. P/L., return address: Wildlife Box 155 North Quay 4002 Qld Australia; Limpus, 1992) were used. The turtles were double tagged, one tag in each front flipper. No attempt was made to tag all turtles ashore in any one night. The measurements taken followed the standard methodology of the Queensland Turtle Research Project as described by Limpus et al. (1983a): midline curved carapace length (CCL); clutch count; egg diameter, egg weight (10 eggs randomly selected per clutch); nest depth to the bottom of the egg chamber; incubation and emergence success of clutches; sand temperature at 50cm depth. Samples of eggs and recently dead hatchlings were collected and deposited in the Queensland Museum.

Air temperature, rainfall and wind data have been obtained from the Bureau of Meteorology (Brisbane) for their weather station at Thursday Island (10°35'S, 142°13'E, 60m elevation, 45km from Crab Island). This is the closest weather station to Crab Island for which there is a comprehensive data set. Tidal data for Booby Island was used (Anon, 1990). Booby Island, 47km to the north west is the closest standard port tidal bench mark across open water to Crab Island.

RESULTS

Study Site

Crab Island (10°59'S, 142°06'E. Fig. 1) is a crescentic sand island that measured 6.2km in length along the high tide level of the outer western beach on 6 July. The inner eastern margin of the island was partly mangrove lined with wide inter-tidal mud flats. The western beach was composed of mixed siliceous sand and calcium carbonate (broken mollusc) fragments and was exposed to surf. Beach rock was exposed intertidally in sectors 4 and 5. The vegetation of the foredune nesting habitat of the western beach was variable: *Melaleuca* woodland with a grass and herb understorey in sectors 5 and 6; open woodland of scattered *Casuarina equisetifolia* (sectors 4 and 7); grassland dominated by *Spinifex hirsutus*, *Ipomoea pes-caprae* and *Tribulus cistoides* (sectors 2-4, 5, 8-10); unvegetated sand dune (sector 6). There were no mangroves growing on the western beach. However, there were standing dead mangrove trunks on the northern part of the western beach that were the result of past encroachment of the island into the mangrove forest. The dead mangroves and beach rock were not an impediment to the nesting activities of the turtles.

Crab Island lies within a region with a distinct summer wet season and winter dry season. The mean monthly rainfall and the mean daily minimum and maximum temperatures for the years 1950-1991 at Thursday Island ranged from 4mm in September to 419mm in January (Fig. 2). Crab Island has no surface freshwater for most of the year. There is an ephemeral freshwater swamp system behind the dune in the northern end of sector 5 which supports at least one species of frog, *Limnodynastes ornatus* (QMJ31755-7). This swamp was dry during the July visit and in most years there would be insufficient rain to refill the swamp until January, which is the peak of the wet season (Fig. 2). Monthly mean daily maximum temperatures ranged from 31.2°C in November to 27.7°C in July, while monthly mean daily minimum temperatures ranged from 25.4°C in December to 22.5°C in July. During the middle of wet season months of January and February the wind is predominantly from the west and northwest and is mostly weaker than 20km/hr. In the middle of dry season months of May to October there are almost no westerly or northwesterly winds; the dry season winds come predominantly

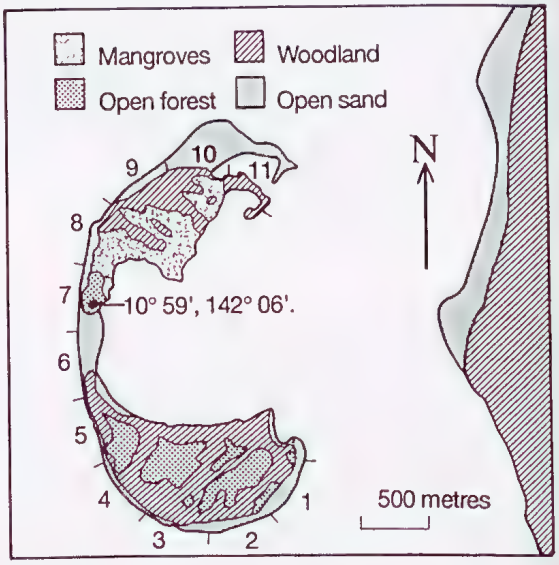

FIG. 1. Map of Crab Island showing position of numbered beach sectors and vegetation types.

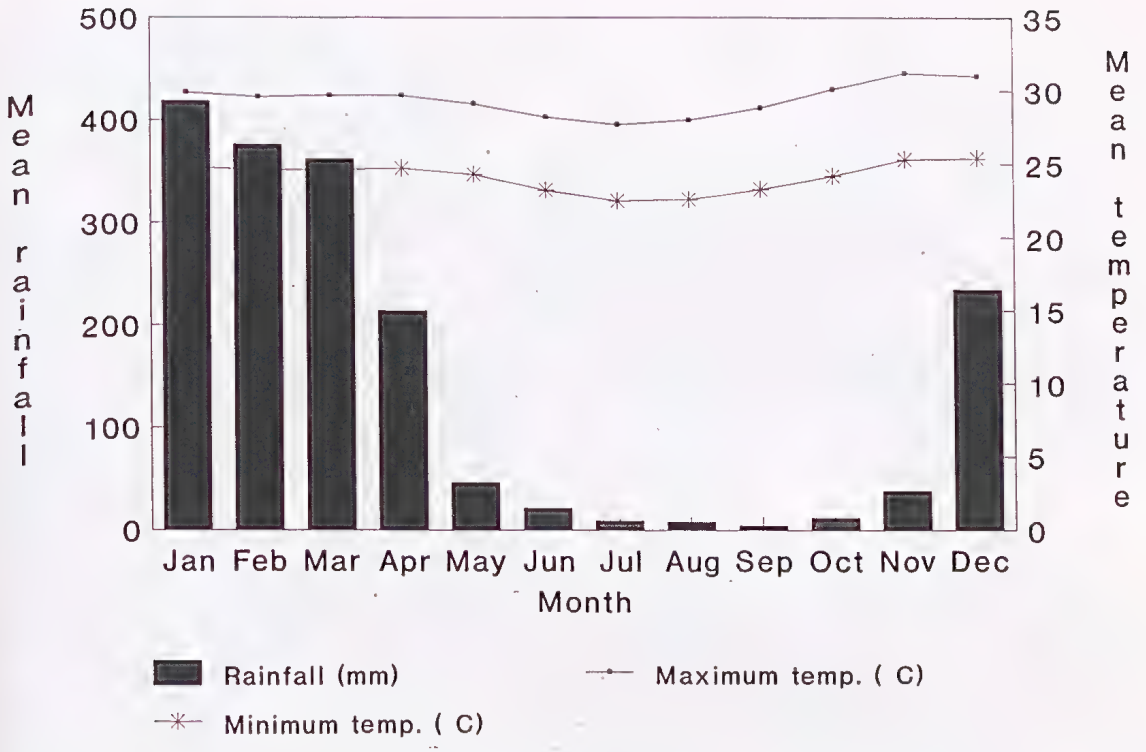

FIG. 2. Monthly mean rainfall (mm) and monthly mean daily minimum and maximum temperatures recorded at Thursday Island Meteorological Station for the years 1950-1991.

from the east and southeast and are mostly stronger than 20km/hr. Mean sand temperature at 50cm depth within the turtle nesting habitat was 27.6°C (SD = 0.49, range = 26.4 - 28.5, n = 44, 1 - 5 measurements per night).

The mean beach width above the spring high tide level was 31.3m (SD = 15.3, n = 10). The narrowest beach (8m) occurred at sector mark 3 and the widest (53m) at sector mark 10. There are two high tides per 24hr at Crab Island (Fig. 3). During 6-22 July, 1991, the daily tidal range varied from 3.46m (12th) to 2.36m (19th). The variation in night time high tide height (0.27m) was less than that of the daytime high tides and both sets of low tides (Fig. 3).

NESTING TURTLES

On the team's arrival at the island on 6 July, 1991, there were 309 turtle tracks visible (174 *N. depressus*, 135 not identifiable to species). Based on nightly track counts from the 14 nights 6-19 July (Fig. 3), there was an average of 132.7 beachings of *N. depressus* per night (SD = 52.11, n = 14, range = 68-235) from a total of 1839 recorded beachings. Similarly, there was an average of 0.6 beachings of *E. imbricata* per night (SD = 0.93, n = 14, range = 0-3) for a total of 9 beachings.

On the limited data from this visit, there is a suggestion that the maximum nightly nesting density may follow the occurrence of afternoon high tides. Only *N. depressus* was recorded coming ashore for nesting during daylight hours (19 [1.0%] of the 1839 total beachings). Most (4 and 13) of these daylight nesting emergences occurred on two days only (8th and 9th July, respectively) with the remainder being single beachings on each of the 10th and 20th July. All except one of the daylight beachings occurred on days with mid-afternoon high tides (8th-10th) while the remainder coincided with a midday high tide (20th).

Turtle nesting activity was restricted to the western (ocean) beach, except for one turtle which came ashore on the western side at the narrow middle of the island (sector 6) and returned to the sea on the eastern side. Most nesting activity occurred within the middle sectors 4-8 (Fig. 4) where the beach width ranged 26-43m. The number of turtle beachings varied nightly and among sectors. The densest activity occurred in sector 5 (nightly mean number of tracks = 43.9,

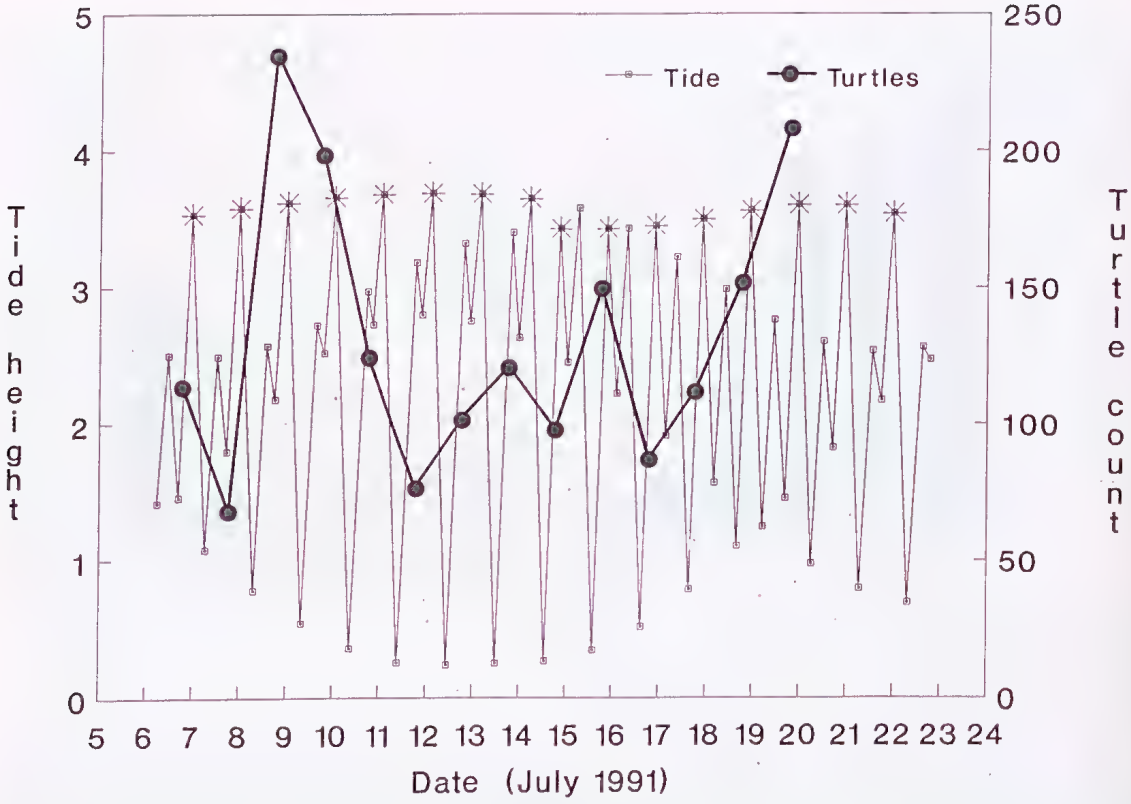

FIG. 3. Daily frequency of beachings by nesting Flatback Turtles, *Natator depressus*, at Crab Island during 6-19 July 1991. The daily variation in tide height (in metres), measured at Booby Island is also shown. *denotes a night time high tide.

SD = 25.49, n = 14, range = 21 - 102) while no tracks were recorded on any night in sector 11.

For the sample of 172 beachings by *N. depressus* examined for nesting success, 132 females (76.7%) definitely laid eggs, 14 (8.1%) could not be determined for nesting success and 26 (15.2%) returned to the sea without laying eggs. Thus there was a probability (±95% confidence limits) of between 76.7±3.2% and 84.8±2.8% that a turtle would successfully lay eggs when she came ashore. When this nesting success probability is applied to the track counts for the period 6-19 July, it is estimated that between 1352 and 1611 *N. depressus* clutches were laid on the island during the 14 nights of observation.

For the sample of 6 beachings by *E. imbricata* examined for nesting success during the same period, 4 laid and 2 did not lay. This represents a nesting success of 67% for this species with an estimated total of 7 clutches laid during the 9 beachings.

Over the 15 nights, 6-20 July, 489 nesting turtles were examined and tagged (483 *N. depressus* and 6 *E. imbricata*). There were no recaptures of any turtles that had been tagged during previous visits to the island, nor were there migrant recaptures of any turtles tagged at other locations. The size distribution of these nesting turtles are summarised in Table 1 and Fig. 5. The mean CCL of the nesting turtles was: *N. depressus* = 88.2 cm, *E. imbricata* = 83.9 cm.

Turtles Adjacent to Beach

By day when the weather was calm during 6-21 July 1991, there were numerous sightings of solitary turtles surfacing to breathe, mostly within 50m of the beach. All were adult sized *N. depressus*. Up to 15 such turtles were observed adjacent to a single sector during a track census with 0-49 isolated turtles seen during a single track census along the entire beach. The water was clear enough at high tide for adult sized *N. depressus* resting on the bottom at 2m depth to be visible from a dingy adjacent to the beach. In addition, mating turtles were observed in the surf adjacent to the beach on four days (0-2 courting pairs per

TABLE 1. Curved carapace length (cm) of nesting female turtles on Crab Island and adjacent beaches since the studies of Limpus et al. (1983a).

Species	Location	Date	Mean	SD	range	n
Natator depressus	Crab Island	15-16 Jan 1991	90.3	2.49	85.0-95.5	18
		06-20 Jul 1991	88.2	2.80	77.0-95.6	315
	mouth of Jardine River	29 Dec 1987	88.8	0.47	88.5-89.5	3
Eretmochelys imbricata	Crab Island	28 Dec 1989	86.0	—	—	1
		06-20 Jul 1991	83.9	2.41	79.5-86.5	6

daily track census). All were mounted pairs of *N. depressus* and no attendant males were observed. One mounted male (B0314) was captured and measured : CCL = 83.1cm, tail length beyond the carapace = 22.0cm (Fig. 6). The adult male *N. depressus* was similar to the adult female (Fig. 7) in most external features: colour, low doming of the carapace along the midline and lateral upwards reflexing of the carapace (Limpus et al., 1988). The only observed external dimorphic characters were tail length (male very long vs female short) and claws (male elongate and strongly recurved vs female short and slightly curved). The male was mounted on the female, venter to dorsum (Fig. 8), and was gripping the female's carapace margin via the single recurved claw on each flipper. The male was mounted well forward on the female such that his head could rest on her anterior carapace and dorsal neck. His snout contacted her head when she raised her head for a breath.

Adult Mortality, Injuries and Diseases

No dead turtles were found along the beach on arrival on 6 July. The highest and narrowest dunes on the island were in sector 4. The 10m high dune front in this area was steep enough for most turtles to have difficulty in climbing it. One female *N.*

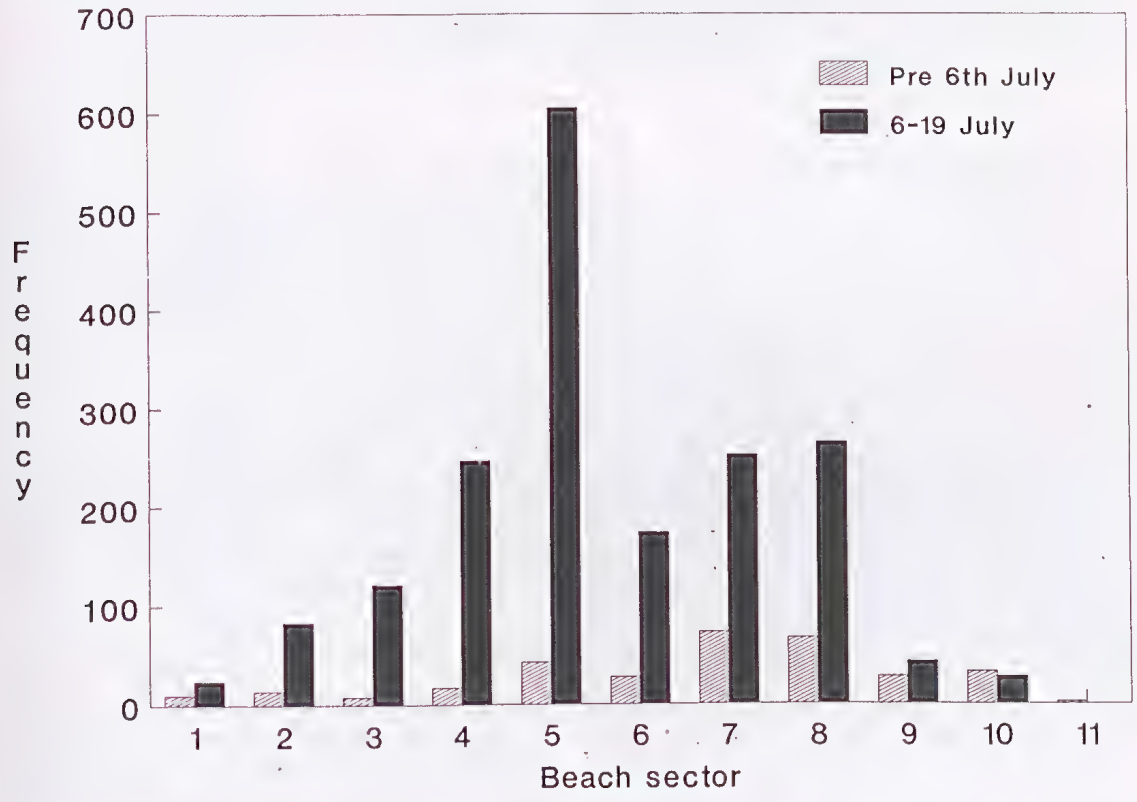

FIG. 4. Distribution of turtle tracks by beach sector on Crab Island, 6-19 July 1991.

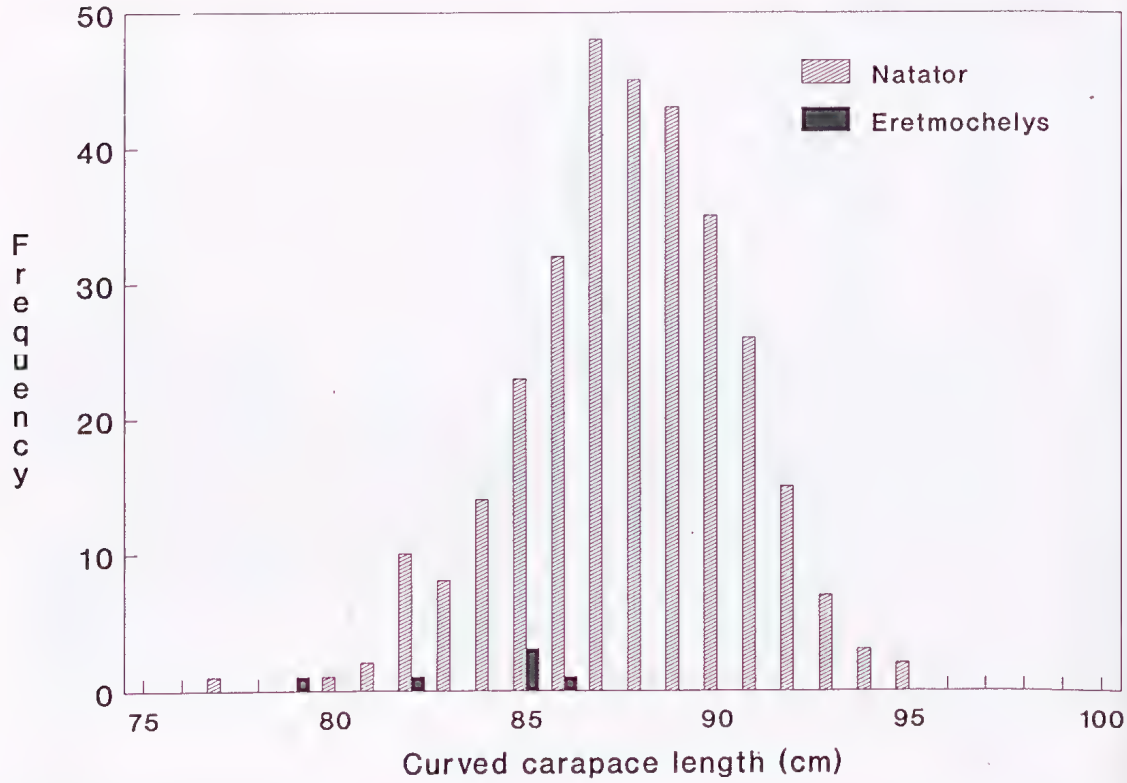

FIG. 5. Size distribution of nesting female *Natator depressus* and *Eretmochelys imbricata* at Crab Island, 6-20 July 1991.

depressus was observed to climb this dune and attempt to nest inland of the dune crest. Later, after wandering to the inland base of these dunes, she was able to find her way back to the beach and return to the sea. A search of the woodland and forest areas inland of the dune crest throughout the island revealed the old fragmented skeletal remains of two adult sized *N. depressus* lying ventral side down behind sector 4. These remains were consistent with the turtles having died after being disoriented following a nesting attempt inland of the crest of the high dunes. No nesting females died while ashore during the 6-21 July 1992 visit.

One large crocodile, *Crocodylus porosus*, (total length 3+m) was observed on most days during late mornings at the water's edge in sector 3. While this crocodile was large enough to be a predator of adult turtles, no turtles showed signs of having been mauled by a crocodile. Several nesting turtles did, however, have healed crescentic damage to the carapace that was presumed to have resulted from past shark or fish bites. For *N. depressus*, loss of large crescentic pieces from the carapace was recorded for 8 (1.7%) turtles, minor carapace damage was recorded for 17 (3.5%) turtles and loss of one third or greater of a flipper was recorded for 32 (6.6%) turtles. All of these injuries were from well before the current nesting season as indicated by their completely healed state. None of the *E. imbricata* showed signs of significant injuries.

Fibropapillomas were recorded on five of the nesting *N. depressus* only: B505, 2 fibropapillomas on neck; B535, 2 on right hind flipper; B625, 1 on right front flipper; B690, 1 on the right shoulder; B1165, 1 on neck. The largest fibropapilloma was 2.4cm in diameter. The ventral surface was not examined.

CLUTCHES

For *N. depressus*, the mean clutch count was 55.9 eggs (Table 2, Fig. 9) and the mean egg diameter was 4.93cm (Table 2). Of the 32 clutches counted at oviposition, one contained one yolkless egg and none contained multiyolked eggs. During the laying of these 32 clutches the

FIG. 6. Adult male Natator depressus, tag number B0314, returning to the sea after being brought ashore for tagging and measurement.

nesting females did not dig into any existing clutches.

For *E. imbricata*, the mean clutch count was 139.3, the mean egg diameter was 3.60cm and the mean egg weight was 26.1g (Table 2). None of the four clutches counted at oviposition contained yolkless or multiyolked eggs. During none of the five successful nestings observed did the turtle dig into an existing clutch.

Representative eggs were collected : 6 normal *N. depressus* eggs, QMJ31745; 1 yolkless *N. depressus* egg, QMJ31747; 3 normal *E. imbricata* eggs, QMJ31746.

Emerged Clutches

Eighty four freshly emerged clutches were identified to species by examination of eggs, hatchlings or hatchling tracks. All were *N. depressus* clutches. Representative hatchling *N. depressus* were collected : QMJ31748-31753. Strong winds prevented the accurate count of emerged clutches for all beach sectors on most nights. Within the relatively wind protected area of sector 5, the nightly number of emerged clutches was counted on 6-15 July. The mean number of *N. depressus* clutches emerging per night in this sector was 4.1 (SD = 2.23, range = 0-8, n = 14 nights, 57 nests). The maximum number of emerged clutches counted along the entire beach on a night with light wind was seven, with four of those in sector five. Hatchlings were often encountered crossing the beach at night but none were seen by day.

Forty nests from recently emerged clutches were dug to assess hatchling incubation and emergence success. After having been laid, two of these clutches had been each dug into by another turtle, representing a clutch disturbance rate after having been laid of 0.05. Another of these 40 emerged clutches had been laid by a turtle that had dug into an existing clutch (clutch disturbance rate at laying = 0.025). Because these latter eggs were adjacent to another previously emerged clutch they could not be counted accurately. Counts were made from the remaining 39 freshly emerged clutches (Table 3). There was no significant difference (t test, $p,<<0.05$) between mean clutch count measured at laying (Table 2) and mean clutch count measured at emergence (Table 3, Fig. 9), the latter having been laid approximately two months earlier. The mean depth to the bottom of these nests was 58.3 cm (Table 3). There were yolkless eggs (1 per clutch) in two of these clutches.

From the 2129 eggs in the 39 clutches counted, there was a mean hatching success of 81.84%, while hatchling emergence from the nest to the beach surface represented 78.56% of the eggs laid (Table 3). Egg mortality was distributed as follows: 10.4% unhatched, 7.4% undeveloped and 0.3% predation by ghost crabs, *Ocypode* sp (3 nests). Within the nests, there were dead hatchlings representing 2.4% of the eggs laid. A further 0.9% of the eggs were represented by live hatchlings that may or may not have escaped from the nests, had they not been excavated. This included 9 hatchlings that were tangled in a buried branch over one nest.

Egg and Hatchling Predation

There was no evidence of known egg predators such as varanid lizards or large mammals (pigs, dogs, cats) on the island.

Nankeen night herons (*Nycticorax caledonicus*) including adults and fledged juveniles were present in the nesting habitat each night and were observed eating hatchling *N. depressus*. These birds were most concentrated in beach sectors 4-5. At night, up to 6 birds were observed around a nest taking hatchlings as they emerged. This

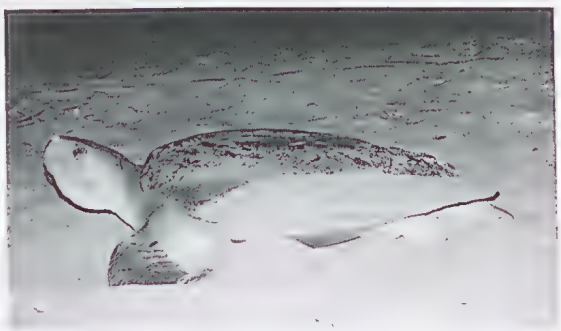

FIG. 7. Adult female *Natator depressus* returning to the sea after nesting on Crab Island.

TABLE 2. Clutch counts and egg measurements recorded from nesting turtles at Crab Island, 6-20 July 1991.* denotes ten eggs measured per clutch.

Species		Mean	SD	range	n
Natator depressus	clutch count	55.9	9.57	34-74	32
	egg diameter(cm)	4.93	0.173	4.52-5.17	60*
Eretmochelys imbricata	clutch count	139.3	10.30	123-151	4
	egg diameter(cm)	3.60	0.071	3.49-3.77	30*
	egg weight (g)	26.08	1.075	24.0-28.0	30*

species was observed also scavenging on turtle eggs that had been dug up by a nesting turtle. Silver gulls (*Larus novaehollandiae*, 1 pair present) flew away with two *N. depressus* hatchlings that had been released from an emerged clutch excavated during the afternoon.

Other potential predators of turtle hatchlings within the nesting habitat and beach area were: water python (*Morelia mackloti*, population estimate not attempted; 1 specimen collected, QMJ31754), estuarine crocodile (*Crocodylus porosus*, minimum of five individuals, including three whose hind foot print lengths were 27, 22.5 and 17.5cm), beach thickknee (*Burhinus neglectus*, several groups of 2-3 birds), osprey (*Pandion haliaetus*, 1 pair), whistling kite (*Haliastur sphenurus*, 1 bird), white breasted sea eagle (*Haliaeetus leucogaster*, 1 pair), frigatebird (*Fregata* sp., 1 bird). Potential predators of turtle hathlings in the adjacent surf included: Australian pelican (*Pelecanus conspicillatus*, flock of 10), numerous small black-tipped whaler sharks (*Carcharhinus* sp.).

On the team's arrival at the island, there were two recently used fire places with broken *N. depressus* egg shells and fish remains in sectors 5 and 7. During the 17 days the team was at the island, three parties of local residents from adjacent mainland communities visited to collect turtle eggs. Turtle nests were located by probing the sand in old body pits with a spear. All three parties directed their egg collecting activity in sectors 5-8, the area of highest density turtle nesting: 14 July three men collected an estimated equivalent of four clutches of *N. depressus* eggs; 17 July a party of adults and children collected multiple clutches of turtle eggs: 21 July three men collected an undetermined number of turtle eggs. On the 22 July, a fourth party from two dinghies visited the island, but the purpose of their visit was not assessed. One of the nests dug on 14 July contained eggs with dried egg shell, i.e. it was not freshly laid. The collector expressed the view that these particular eggs were of marginal quality for eating and only half of the clutch was taken and the remainder reburied.

Other Incidental Data

During a visit on the night of 29 December 1987 to the south of the Jardine River mouth, three *N. depressus* were tagged in the first 100m and several others could be seen further along the beach (E. Evans, in litt.). G. Kyriazis (pers. comm.) walked the beach along the mainland coast from 1 to 3km south of the mouth of the Jardine River during early September 1991. His impression of the track density at this time was that it was comparable to the track density on Crab Island in July 1991. There was one freshly dead *N. depressus* that had died on its return crawl to the sea after nesting. Pigs were recorded to have destroyed most of the hundreds of turtle nests seen on a 6km section of this mainland beach in the early 1980s (B. Gray, pers. comm.) and local residents continue to identify pig, dingo and varanid predation of eggs as common on this beach (G. Kyriazis, pers. comm.). The size range of female turtles tagged while nesting on other occasions during 1987-1991 at Crab Island (n = 19) and the Jardine River mouth (n = 3) are summarised in Table 1. The majority of turtles encountered on these occasions were *N. depressus*.

Recaptures

One long distance migration has been recorded from these taggings. An adult female *N. depressus* (T40505), which had been tagged while nesting at Crab Island on 15 January 1990, was captured in a fishing net off Merauke (8°30'S, 140°22'E) in southern Irian Jaya on 10 January

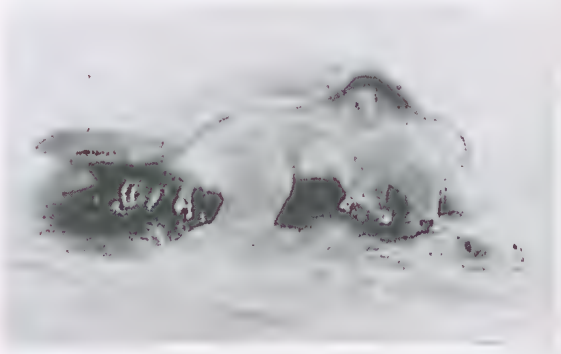

FIG. 8. Adult male *Natator depressus*, tag number B0314, mounted on female prior to capture in approximately 0.7m deep water adjacent to the beach. The female has just surfaced for a breath.

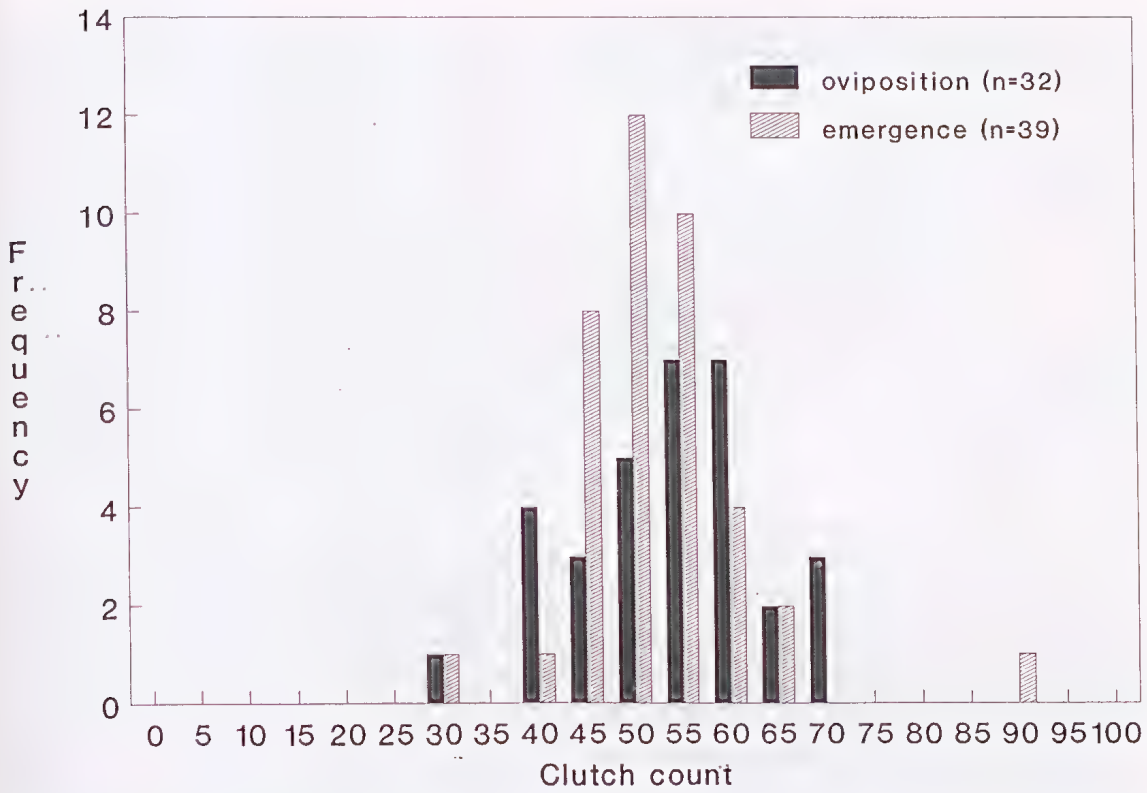

FIG. 9. Frequency distribution of *Natator depressus* clutch counts measured at oviposition and at clutch emergence, Crab Island 6-20 July 1991.

1992. This turtle was eaten. The recapture was made 310km from the nesting beach and two years after she was tagged. This is the first record of *N. depressus* from the coastal waters of Irian Jaya.

One remigration recapture has been recorded from these taggings. *N. depressus* (B1181) was recorded nesting back at Crab Island on 11 September 1992, approximately fourteen months after her initial tagging at Crab Island on 20 July 1991.

DISCUSSION

Marine turtle nesting at Crab Island was first quantified in November-December 1970 (Bustard, 1972). There were subsequent brief visits to further quantify nesting density and to tag nesting turtles during 1976-1979 (Limpus et al., 1983a). As a result of these surveys, Crab Island was found to support all year round breeding and was identified as supporting the largest recorded *N. depressus* nesting population. Low density *E. imbricata* and sporadic *Lepidochelys olivacea* nesting was also recorded for the island. Specimens of *N. depressus* were collected from Crab Island in January 1981, but the nesting population was not described (Zangerl et al., 1988). The island has remained unsurveyed for marine turtles since August 1979. Limpus et al. (1989) identified that *N. depressus* nesting occurs widely in western Torres Strait, with another large nesting concentration at Deliverance and Kerr Islands. The results of the present study allow for a re-evaluation of the status of this significant turtle rookery after 12 years.

Marine turtles typically lay multiple clutches within a single nesting season at approximately two weekly intervals, except for *Lepidochelys* spp. (Hirth, 1980; Limpus et al., 1984). Not all individuals in a particular population begin or complete nesting at the same time of the year (Limpus, 1985). At rookeries in eastern Australia where *Caretta caretta* and *Chelonia mydas* have a discrete nesting season, 60-70% of the total nesting population for the year can be expected to be recorded during a two week tagging census at

TABLE 3. Incubation and emergence success recorded from 39 freshly emerged *Natator depressus* clutches excavated for counting on Crab Island, 6-22 July 1991.

		Mean	SD	n	range
emerged hatchlings		42.9	12.99	39	17-87
hatchlings in nest:	live	0.5	1.73	39	0-10
	dead	1.3	2.51	39	0-11
eggs	unhatched	5.7	5.98	39	0-22
	undeveloped	4.1	5.10	39	0-30
	predated	0.2	0.59	39	0-3
clutch count		54.6	9.37	39	34-94
nest depth (cm)		58.3	7.21	36	43-71
Hatching success %		81.84	17.29	39	26.5-100.0
Emergence success %		78.56	18.55	39	25.0-100.0

the peak of the nesting season (Limpus, 1985 and unpublished data). Therefore a two week census of the Crab Island nesting population at the peak of the nesting season also is presumed to sample a similar proportion of the total population. However, there is all year round nesting at Crab Island (Limpus et al., 1983a) and the present study may not have sampled at exactly the peak of the nesting season. Each of these factors would reduce the proportion of the total population sampled during the two week census. Therefore, the estimated 1352-1611 clutches laid during the 14 nights, 6-19 July 1991, indicate that in excess of 2200 female *N. depressus* were breeding at Crab Island during the 1991 breeding season. While there are insufficient data to identify any changes in the size of this nesting population since it was last surveyed during 1976-1979 (Limpus et al., 1983a), Crab Island continues to support the largest recorded breeding aggregation for this marine turtle. However, it should be remembered that many *N. depressus* nest on the adjacent mainland and that the species also nests on the islands extending to the north throughout western Torres Strait (Limpus et al., 1989). The total annual breeding population for *N. depressus* in the Crab Island region (northeastern Gulf of Carpentaria and western Torres Strait) remains imprecise, but must number many thousands of females. There is still no evidence that Crab Island is of anything but minor importance for nesting by other marine turtle species.

As of March 1993, there has been only one reported feeding ground recapture, a female *N. depressus* from the south eastern Irian Jaya coast, out of the many turtles tagged while nesting in the Crab Island region (1040 *N. depressus*, 11 *E. imbricata*, 1 *L. olivacea*: Bustard, 1972; Limpus et al., 1983a; present study). There have been more than 50 recaptures of *N. depressus* reported from the east coast prawn fishery from inside the Great Barrier Reef (GBR) and central Torres Strait, which had been tagged while nesting at the central Queensland rookeries (Limpus et al., 1983b; C. J. Parmenter, pers. comm.). This suggests that the *N. depressus* population nesting at Crab Island does not migrate from the feeding areas along the eastern Queensland coast. No tagged *N. depressus* from Crab Island has been reported from the northern prawn fishery of the Gulf of Carpentaria and southern Arafura Sea even though several thousand *N. depressus* are captured annually as part of the by-catch of the northern prawn fishery (Poiner & Harris, 1993). This lack of *N. depressus* tag recoveries within the northern prawn fishery contrasts with the occurrence of tag recoveries of *C. caretta* from eastern Australian rookeries in the same fishery (Limpus et al., 1992; Limpus & Reimer, 1993). This suggests that the Gulf of Carpentaria is not a significant feeding area for the *N. depressus* that nest at Crab Island. The one long distance tag recovery demonstrates that the feeding distribution of the Crab Island nesting population extends northwards at least to the southern Irian Jaya coast.

Turtle nesting and hatchling emergence have been recorded at Crab Island on all previous visits (April, May, July, August, November and December) with a seasonal variability in density (Limpus et al., 1983a). The limited data from 1991 also show seasonal variability in nesting density. The high density nesting in July (average 133 beachings per night on the whole beach and

44 beachings per night in sector 5; 77-85% nesting success) contrasts with the low number of clutches emerging at the same time (average 4 emerging clutches per night in sector 5). Because the incubation time for marine turtle eggs is approximately two months, in the absence of evidence of extensive clutch destruction or harvest at Crab Island, these data suggest that the July 1991 nesting density was approximately 10 times the magnitude of the nesting density two months earlier in May 1991. The 6-19 July 1991 nesting density appears to be considerably greater than the density recorded in 15-19 July 1978 but included nights with similar nesting density to that recorded on 13-14 August 1979 (Limpus et al., 1983a). This apparent increase in nesting population as indicated by the July nesting densities could have three different explanations: 1, this between-year vari

ability could be the result of natural annual fluctuations in the nesting population as has been recorded for *C. mydas* in eastern Queensland (Limpus & Nicholls, 1988); 2, the timing of the peak of the nesting season may vary between months in different years; 3, there may have been an increase in the size of the nesting population. Because of the high fidelity that *N. depressus* displays to particular small nesting beaches (Limpus et al., 1984) the possibility that the apparent increase in the Crab Island nesting population could have resulted from inter-rookery movements is dismissed. More extensive surveys of the rookery are needed before the stability of this population can be reliably assessed. Given the extended breeding season and the wide nesting distribution in western Torres Strait, Crab Island and northwestern Cape York Peninsula, the size and distribution of the breeding population cannot be adequately surveyed by brief visits to single localities as has been the pattern to date.

The data collected on this survey of *N. depressus* from Crab Island (Tables 1,2) provide additional support for the conclusion that the *N. depressus* nesting population from the Crab Island region consists of smaller nesting females laying comparable sized clutches of smaller eggs than those of the nesting population at the southern GBR rookeries (Limpus et al., 1989). The hatchling productivity from undisturbed clutches at Crab Island remains comparable to that recorded in previous studies (Limpus et al., 1983a).

The mid-year high density *N. depressus* nesting and associated incubation of eggs at Crab Island spans the months of lowest rainfall and daily air temperature (Fig. 2). This dry season nesting also coincides with the predominantly south easterly winds. Therefore the majority of the turtle nesting occurs on beaches with a westerly aspect; these are usually leeward to the prevailing winds and are therefore less likely to be eroded by wind driven surf when most eggs are incubating. Also, by nesting in the dry season, the turtles might be avoiding egg loss through flooding that could result from a raised water table below the dunes during the wet season.

The sand temperature (mean±SD) at 50cm depth in the nesting habitat for 6-21 July 1991 of 27.6±0.49°C was the lowest recorded in any month at Crab Island (12 Dec. 1976 = 29.6± 1.32°C, 8-10 Dec. 1978 = 31.4±0.88°C, 27 April-7 May 1978 = 29.4±1.21°C. Limpus et al., 1983a) or at Deliverance Island (2-4 October 1987 = 29.4±0.95°C. Limpus et al., 1989). However, the year round sand temperatures at nest depth in the Crab Island area remain above 24°C, the approximate lower limit for successful incubation of marine turtle eggs from all species (Miller, 1985). This facilitates the observed all year round successful nesting by marine turtles in the Crab Island region, although the mid-summer sand temperatures approach 34°C which is the approximate upper lethal incubation temperature for marine turtle eggs (Miller, 1985). In contrast, at the rookeries in central and southern Queensland, the winter sand temperatures at nest depth fall below 24°C and consequently, successful marine turtle nesting can only occur there during the warmer summer months (Limpus, 1971; Limpus et al. 1981). In northern Australia there has probably been a selective advantage for marine turtles to aggregate their nesting into the mid-year when sand temperatures are well separated from the lethal limits of incubation temperature (Guinea 1993).

The pivotal temperature, the theoretical temperature at which a 1:1 sex ratio could be expected, is not fixed for *Caretta caretta* or *Chelonia mydas* but varies between breeding units. While within each breeding unit, the species reproduces regionally on beaches that provide a range of nest temperatures spanning the pivotal temperature (Limpus et al., 1983c; C. Limpus, unpublished data). The pivotal temperature for *N. depressus* from the southern GBR region is 29.5°C, ranging from 100% male hatchling production at 28°C to 100% females at 31°C (C. Limpus, unpublished data). Based on the recorded sand temperatures at Crab Island (see above), if the Crab Island region population had

the same pivotal temperature as the southern GBR population, Crab Island would be producing mostly male hatchlings during the mid-year high density nesting, while mostly females would be produced from the low density summer nesting. However, if the Crab Island region nesting population is part of a separate breeding unit from the southern GBR population, then different pivotal temperatures could occur for the populations. This would then allow for the possibility of the Crab Island nesting population fitting the model that a turtle breeding unit chooses its nesting beaches such that its pivotal temperature occurs within the range of sand temperatures at nest depth that is available during the main nesting season. This would require that the Crab Island region and southern GBR nesting populations represent different *N. depressus* breeding units. The differences in adult and egg size between the northeastern Gulf of Carpentaria and southern GBR *N. depressus* populations also support the hypothesis that these populations are separate stocks. A precise estimate of the *N. depressus* hatchling sex ratio from Crab Island cannot be made from the available data.

The local peoples of northern Cape York Peninsula, western Torres Strait and Irian Jaya harvest small numbers of adult *N. depressus* and numerous clutches of eggs annually from this population (Johannes & MacFarlane, 1991; Limpus et al., 1983a, 1989; present study). The impact of each of these village-based harvests should not be considered in isolation. Indeed, the harvest at any one nesting beach or by any one village should be assessed within the regional context of the total breeding population. In relation to this, the significance of egg losses through harvest and predation to the regional population poses major uncertainties. If the mainland beaches have a different sand composition and hence sand colour, they would have a different temperature profile from the islands. In particular, darker sands would be warmer and result in a higher proportion of females from these mainland beaches (c.f. the situation for *Caretta caretta* in southeastern Queensland, Limpus et al., 1983c). The indicated high predation levels by pigs, dingoes and varanid lizards on the eggs laid on the mainland beaches has the potential for threatening the survival of the entire population in the long term. The observed egg harvest by local people of a few clutches each week from Crab Island could be sustainable during the mid-year high density nesting. However, if the rate of harvest is constant throughout the year and the off-peak nesting produces mostly female hatchlings, then the loss of additional female hatchling production through egg harvest must be considered in conjunction with the impact of the egg predation on mainland clutches. In addition, what impact the drowning hundreds of *N. depressus* annually in fishing gear in the northern prawn fishery (Poiner & Harris, 1993) and other Gulf of Carpentaria fisheries (P. Couper, unpublished data) has on the Crab Island nesting population needs clarification. These *N. depressus* mortalities in the dispersed feeding areas represent additional losses to this population that have commenced in recent decades. Before it can judged as to whether the current level of harvest of *N. depressus* eggs and turtles by the local peoples from these rookeries of the northeastern Gulf of Carpentaria and western Torres Strait is sustainable, the breeding unit of these turtles needs to be aligned to geographic boundaries and population size and anthropomorphic mortality for the population throughout its range quantified. In addition hatchling productivity and associated sex ratio should be quantified from the significant rookeries within the region. When these types of data are available, the long term viability of this most significant *N. depressus* population and the associated harvests can be more reliably assessed.

ACKNOWLEDGEMENTS

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PANDARID COPEPODS PARASITIC ON SHARKS FROM NORTH QUEENSLAND WATERS. *Memoirs of the Queensland Museum 33(1): 290. 1993:-* The Pandaridae are ectoparasitic caligoid copepods exclusive to elasmobranchs. 38 species are known worldwide (Cressey, 1967, 1970; Rangnekar & Rangnekar, 1972; Cressey & Boyle, 1978; Cressey & Simpfendorfer, 1988).

In a checklist of fish parasites from Australian waters, Beumer et al. (1983) listed 8 pandarid species based on records in two published studies of Australian copeopod parasites (Heegaard, 1962; Kabata, 1966). Beumer et al. (1983) followed Cressey (1967) in synonymising *Dinematura* Burmeister, 1833 with *Dinemoura* Latreille, 1829. However, they did not follow Cressey by regarding *Nesippus australis* Heegaard, 1962 and *N. incisus* Heegaard, 1962 as separate from *N. orientalis* Heller, 1868, or by regarding *Perissopus serratus* Heegaard, 1962 as separate from *P. dentatus* Steenstrup & Lütken, 1861. Beumer et al. (1983) thus contained 6 valid species: *Dinemoura latifolia* (Steenstrup & Lütken, 1861), *D. producta* (Müller, 1785), *Echthrogaleus coleopratus* (Guérin-Méneville, 1837), *Nesippus orientalis* Heller, 1868, *Pandarus bicolor* Leach, 1816, and *Perissopus dentatus* Steenstrup & Lütken, 1861. Cressey & Simpfendorfer (1988) added *Pseudopandarus australis* to the species known from Australian waters. This note reports the occurrence of 3 pandarid species on sharks from Cleveland Bay (19°15'S, 146°50'E), north Queensland, and provides information on their hosts. Sharks were caught between Feb. 1986 and Jan. 1988 using gillnets, longlines, otter trawls and handlines. The parasites were identified using keys in Yamaguti (1963) and Cressey (1967).

Three species were identified: *Pandarus niger* Kirtesinghe, 1950 (QMW12207, 12212); *Perissopus dentatus* Steenstrup & Lütken, 1861 (QMW12208, 12209, 12456, 12462, 12464); and *Pseudopandarus australis* Cressey & Simpfendorfer, 1988 (QMW12210, 12211). The occurrence of *P. niger* is a new record for Australian waters. It has previously been reported from Sri Lanka (Kirtesinghe, 1950) and Taiwan (Cressey, 1967) on sharks from the family Carcharhinidae. It is widespread in tropical Australian waters, regularly occurring on *C. sorrah* in the Northern Territory (J. Lyle, pers. comm.; QMW12460, 12461).

Sharks	Specimens examined	*Pandarus niger*	*Perissopus dentatus*	*Pseudopandarus australis*
Carcharhinus dussumieri	16	-	100	12.5
C. fitzroyensis	30	-	50	-
C. macloti	1	-	-	-
C. sorrah	28	21.4	21.4	-
C. tilstoni	45	-	91.4(2.2)	
Rhizoprionodon acutus	47	-	-	61.7(2.1)
R. taylori	201	-	1.0	36.8(3.0)
Hemigaleus microstoma	4	-	75	25(25)
Sphyrna lewini	91	1.1	10.6	1.1
S. mokarran	1	-	100	-

Table 1. Rates of occurrence of pandarid copepods on sharks of Carcharinidae(C), Hemigaleidae(H), and Sphyrnidae (S). Rates given are for females; where present, rate for males given in brackets.

P. dentatus is abundant and widespread in tropical and subtropical oceans, and previous workers have reported it from 29 species of shark (Yamaguti, 1963; Cressey, 1967, 1970; Hewitt, 1967; Russo, 1975; Beumer et al., 1983). Only one of the 8 host species of *P. dentatus* recorded for Cleveland Bay (*Sphyrna lewini*) has previously been reported (Hewitt, 1967).

Rates of occurrence were variable between both host and pandarid species, with female pandarids occurring more frequently, and on more host species, than males (Table 1). The three families of sharks on which the pandarids were recorded are all active, free swimming and closely related (Compagno, 1988). Two benthic shark species (*Chiloscyllium punctatum* and *Stegastoma fasciatum*) — from a different order — had no pandarids on them.

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A HUMPBACK WHALE CALF AND TWO SUBADULT DENSE-BEAKED WHALES RECENTLY STRANDED IN SOUTHERN QUEENSLAND

R.A. PATERSON, C.J. QUAYLE AND S.M. VAN DYCK

Paterson, R.A., Quayle, C.J. & Van Dyck, S.M. 1993 06 30: A Humpback Whale calf and two subadult Dense-beaked Whales recently stranded in southern Queensland. *Memoirs of the Queensland Museum* **33**(1): 291-297. Brisbane. ISSN 0079-8835.

A new born Humpback Whale calf (*Megaptera novaeangliae*) and two subadult Dense-beaked Whales (*Mesoplodon densirostris*) recently stranded on the southern Queensland coast. The *M. densirostris* skeletons were recovered together with various soft tissue material. The post-cranial skeleton of the *M. novaeangliae* was not recovered. The larynges of the three specimens were examined in detail. □ *Humpback Whale, Dense-beaked Whale, stranding, Queensland.*

R.A. Paterson & S.M. Van Dyck, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; C.J. Quayle, Brisbane Clinic, 79 Wickham Terrace, Brisbane, Queensland 4000, Australia; 2 December, 1992.

Opportunities to examine stranded balaenopterid and ziphiid whales, with the exception of Minke Whales (*Balaenoptera acutorostrata*), on the Queensland coast are limited (Paterson & Van Dyck, 1990, 1991). Recently, material recovered from a new born Humpback Whale *Megaptera novaeangliae* and two subadult Dense-beaked Whales *Mesoplodon densirostris* was a valuable addition to the cetacean collection in the Queensland Museum. The *M. novaeangliae* specimen is registered JM8658 and the *M. densirostris* specimens are registered JM8807 and JM9640.

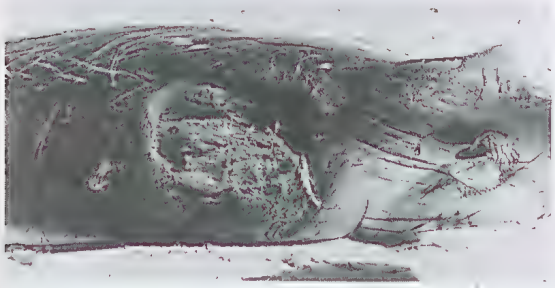

FIG. 1. Shark bites on left side of *Megaptera novaeangliae* JM8658. The anterior bite extended deeply into the thoracic muscles.

SPECIMEN DESCRIPTIONS

HUMPBACK WHALE

JM8658 was a 4.7m long new born (umbilicus unhealed) female that stranded alive during the afternoon of 19 July, 1991 at Eager's Creek (27°07'S, 153°27'E) on the oceanic shore of Moreton Island. Two large non-bleeding shark bites were noted on the left side of the body as

FIG. 2. Extensive superficial rakes on *Megaptera novaeangliae* JM8658. They are considered to be caused by sharks.

well as numerous superficial rakes (Figs 1,2). The whale was refloated and pushed into the surf but was found dead at the same location a few hours later. We examined the carcass three days later. The larger of the previously noted bites extended deeply into the thoracic muscles and its edges showed signs of early healing indicating that the shark attack was not an immediate pre-stranding event.

Material collected included the skull and mandible, blubber and skin samples (the latter for

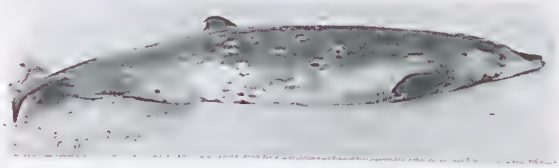

FIG. 3. Recent and healed 'cookie-cutter' lesions on *Mesoplodon densirostris* JM8807.

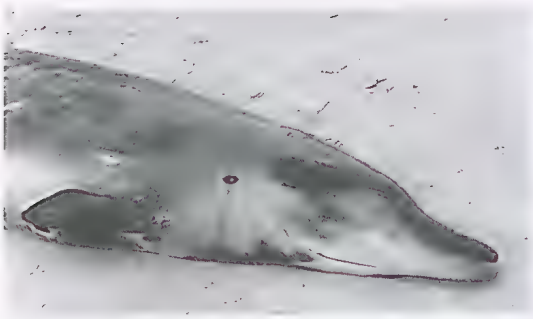

FIG. 4. Close-up view of 'cookie-cutter' lesions on *Mesoplodon densirostris* JM8807. The throat groove characteristic of ziphiids is also demonstrated.

DNA study) and the larynx. The mid-dorsal blubber thickness was 2.8cm and is consistent with recent birth. Comparative blubber thicknesses from a *M. novaeangliae* calf, approximately four weeks old, and a yearling in the Queensland Museum collection are 4.5cm and 9.7cm respectively. The right baleen row numbered 340 ± 5, consistent with the range for the species (Matthews, 1937). The largest baleen plates measured 8.5cm in length.

The stranding of a new born *M. novaeangliae* at latitude 27°S in July confirms previous sighting reports (Chittleborough, 1965; Paterson & Paterson, 1984, 1989) that occasional calving occurs during the northern migration of the species along the Australian coast at latitudes higher than those

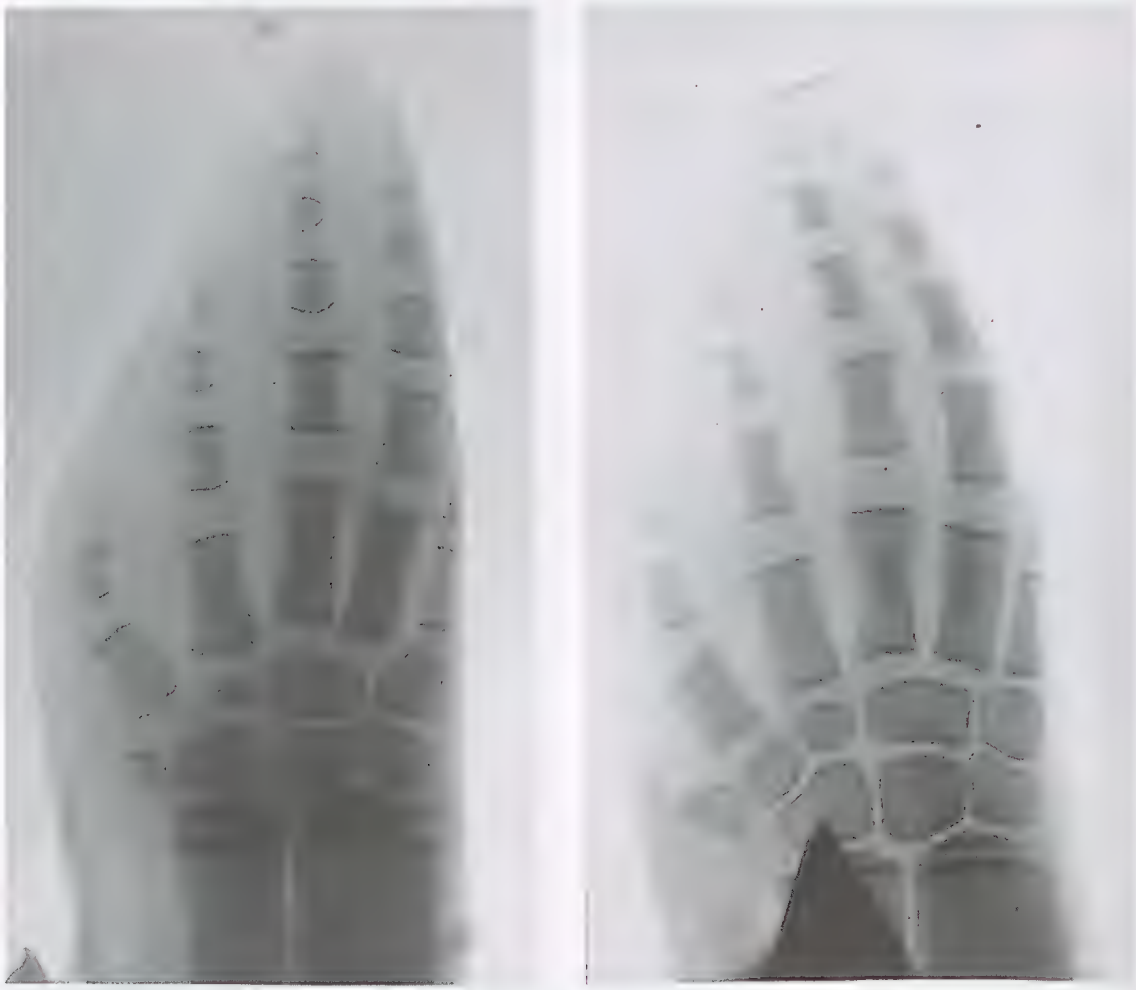

FIG. 5. Left, *Mesoplodon densirostris* JM8807. Radiograph of left pectoral flipper demonstrating distal aspects of radius and ulna, carpus, metacarpals and phalanges. Skeletal immaturity is evident. The ossification centre for the peripheral unciform has not yet appeared. Right, *Mesoplodon densirostris* JM9640. Radiograph of left pectoral flipper showing eight carpal bones compared with seven in JM8807. (The triangular structure overlying the distal ulna is frozen soft tissue from the axillary region.)

at which calving is generally considered to occur (Chittleborough, 1953; Simmons & Marsh, 1986; Townsend, 1935).

Dense-beaked Whales

JM8807 was a 3.8m long female found dead at dawn on 22 October, 1991 at Main Beach, Point Lookout (27°26'S, 153°33'E) on North Stradbroke Island. Recent and healed superficial 'cookie-cutter' lesions were noted and they coalesced ventrally (Figs 3,4). They were similar to, but not as extensive as, those noted in a mature male *M. densirostris* described by Paterson & Van Dyck (1990). The whale was dark grey dorsally and lighter grey ventrolaterally, particularly in the umbilical and genital regions and around the V-shaped throat groove characteristic of ziphiids.

We examined the carcass the day after its discovery. The entire skeleton was collected. The vertebral formula C7; T9; L10; Cdl8=44 is less than counts of 46 and 47 in two *M. densirostris* from the Atlantic coast of North America and 45 in a specimen from Lord Howe Island (Raven,

FIG. 6. *Mesoplodon densirostris* JM8807: left, dorsal aspect of skull; right, dorsal aspect of mandible.

FIG. 7. *Mesoplodon densirostris* JM8807. Left lateral mandibular radiograph demonstrating unerupted tooth characteristic of females.

1942) but is within the range described by Ross (1984). The size discrepancy between the penultimate and last caudals suggests the possibility that one caudal was lost during preparation. With the exception of the coalesced proximal three cervical vertebrae, the central epiphyses of all vertebrae were unfused. The phalangeal formula, derived from a radiograph of the left pectoral flipper (Fig. 5), is I:1, II:4, III:4, IV:3, V:2, which differs slightly from that reported by Kasuya & Nishiwaki (1971) in a Formosan specimen of *M. densirostris*. They (p.133 & fig.1) appear to have included the metacarpals in the formula. The skull and mandible are shown in Fig. 6. The characteristically shaped unerupted mandibular tooth of female *M. densirostris* is demonstrated radiographically in Fig. 7. The tooth measured 52mm in height, 30mm in length and 9mm in greatest diameter. Its pulp cavity was completely unfilled.

Moderate nematode (*Anisakis* sp.) and acanthocephalan (*Bolbosoma vasculosum*) infestation was noted in the stomach and intestine respectively. The gastro-intestinal tract was otherwise empty.

One ovary was collected. Its external features are shown in Fig. 8. Histological examination was reported as follows:

The ovary contains numerous primordial follicles, a few secondary follicles, occasional cystic atretic follicles and some small hyaline scars which may represent corpora albicans. No corpora lutea can be identified.

The presence of secondary follicles indicates sexual maturity is, at least, approached. It is uncertain whether ovulation has occurred. If the small scars are true corpora albicans this would indicate that ovulation had taken place but the evidence is insufficient to establish this with certainty.

Although the ovarian histological evidence indicates that this 3.8m long animal was approaching sexual maturity, the lack of epiphyseal fusion indicates physical immaturity. The dental, sexual and physical development of JM8807 was similar to that of the 3.56m long Formosan specimen described by Kasuya & Nishiwaki (1971).

JM9640 was a 3.65m long female found dead during the morning of 21 June, 1992 at Cathedral

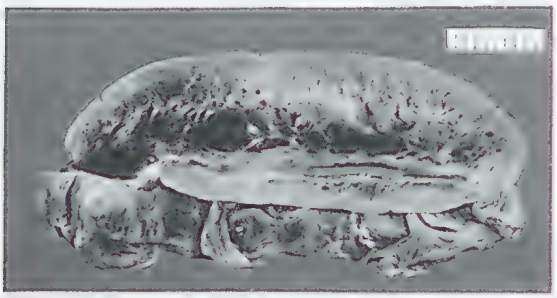

FIG. 8. *Mesoplodon densirostris* JM8807. External ovarian features. Scale in mm.

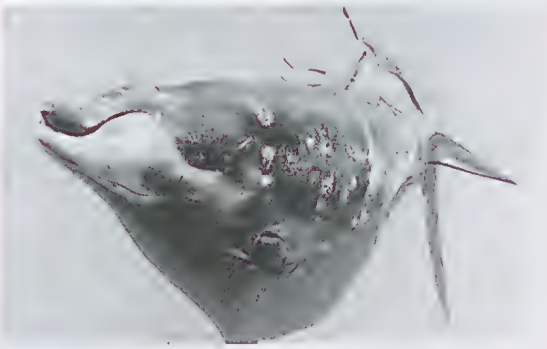

FIG. 9. 'Cookie-cutter' lesions and characteristic throat groove of ziphiids on *Mesoplodon densirostris* JM9640.

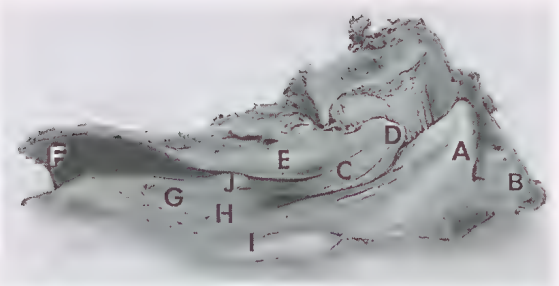

FIG. 10. Larynx *Megaptera novaeangliae* JM8658 in longitudinal section, medial aspect, with thyroid cartilage removed: (A) epiglottic cartilage; (B) fibrous attachment to thyroid cartilage; (C) arytenoid cartilage-corpus; (D) arytenoid cartilage-rostral end; (E) cricoid cartilage; (F) tracheal lumen; (G) fundus of ventral diverticulum; (H) neck of the ventral diverticulum; (I) thyroarytenoid muscle; (J) interarytenoid fibro elastic connection.

Beach (25°10'S, 153°13'E) on Fraser Island. 'Cookie-cutter' lesions of similar distribution to those on JM8807 were evident as well as the characteristic throat groove (Fig. 9).

We were unable to visit the stranding site to examine the whale but arranged for its head and a pectoral flipper to be removed and frozen so that they could be subsequently studied in a fresh state. The remainder of the carcass was buried in sand dunes behind the beach and the skeleton was retrieved two months later. The vertebral epiphyseal status and vertebral formula (C7; T9; L10: Cdl8 = 44) were identical to JM8807 but the last caudal may have been lost. Unfortunately numerous rib and vertebral fractures had occurred during transportation of the carcass to the sand dunes and those fractures detract from the specimen's quality.

The phalangeal formula I:1, II:4, III:4, IV:3, V:2 is identical to JM8807. The carpus contains eight bones (Fig. 5) compared with seven in JM8807 and the Formosan specimen. Raven (1942) demonstrated eight carpal bones in an adult male *M. densirostris*. We presume that the ossification centre of the peripheral unciform had not yet developed in either JM8807 or the Formosan specimen but are surprised at the apparent late development of this bone which is larger than its neighbours in both JM9640 and the specimen illustrated by Raven (1942).

The left tooth measured 54mm in height, 47mm in length and 10mm in greatest diameter. Its pulp cavity was extensively obliterated. On the basis of the dental and carpal development we conclude that JM9640 was more mature than JM8807.

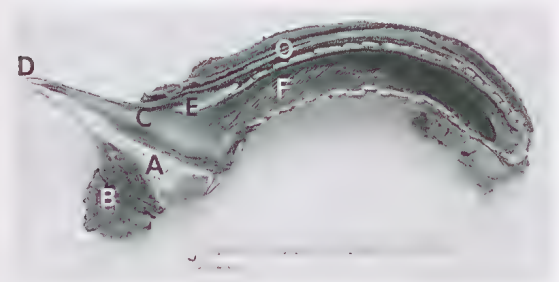

FIG. 11. Larynx *Mesoplodon densirostris* JM8807 in longitudinal section, medial aspect, with thyroid cartilage removed. (A) epiglottic cartilage; (B) fibrous attachment to thyroid cartilage; (C) arytenoid cartilage-corpus; (D) arytenoid cartilage-rostral end; (E) cricoid cartilage; (F) tracheal lumen; (O) oesophagus.

Laryngeal Structure

Various authors, including Benham (1901) and Hosokawa (1950), have compared the larynges of mysticetes and odontocetes. The former are characterised by a large ventral diverticulum surrounded by the thyro-arytenoid muscle and the latter by the aryteno-epiglottideal tube, an upward extension of the fused arytenoid and epiglottic cartilages into the choana. Those features have been demonstrated in JM8658, JM8807 and JM9640.

FIG. 12. Larynx and oesophagus *Mesoplodon densirostris* JM8807 from dorsal aspect. The bossed tip of the aryteno- epiglottideal tube is shown on the right. (C) arytenoid cartilage-corpus; (D) arytenoid cartilage-rostral end; (F) trachea; (O) oesophagus.

The larynx of JM8658 is shown in longitudinal section in Fig. 10 and the salient anatomical structures have been annotated in conformity with the description by Quayle (1991) of the larynx of a male *M. novaeangliae* of similar development to JM8658. There is no appreciable difference between those male and female specimens.

Quayle (1991) considered that phonation could occur between the apposing arytenoids in mysticetes although true vocal cords were not evident. He also proposed a functional role for the ventral diverticulum in the production of the complex sounds of *M. novaeangliae*. Mysticetes presumably generate high pressures within the oral cav-

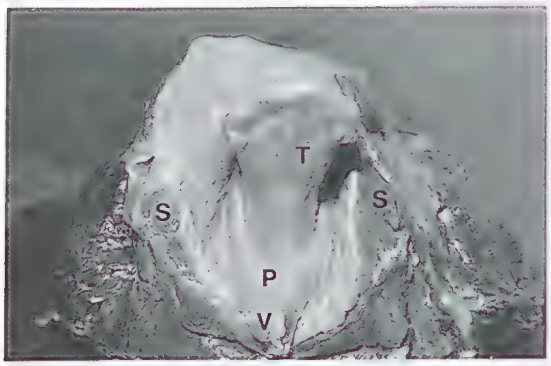

FIG. 13. Laryngo-pharynx *Mesoplodon densirostris* JM9640 from rostral aspect. (P) palato-pharyngeus; (S) superior constrictor of pharynx; (T) aryteno-epiglottideal tube; (V) vomerine attachment of palato-pharyngeus.

ity and pharynx during feeding when large volumes of water are forced through the baleen. The ventral diverticulum may have an additional function in assisting to prevent water from entering the trachea.

The larynx of JM8807 is shown in longitudinal section (Fig. 11) as well as from its dorsal aspect (Fig. 12). The aryteno- epiglottideal tube is bossed at its tip and was closely applied to the posterior narial canal. The almost complete fusion of the arytenoid and epiglottic cartilages and their relationship to the posterior nares more effectively separates the aero-digestive tracts in this odontocete compared with JM8658.

The fresh laryngo-pharynx of JM9640 is shown in Figs 13,14,15. In Fig. 13 the aryteno-epiglottideal tube is demonstrated from the rostral aspect and a large muscular cuff (the superior constrictor of the pharynx) is noted peripherally. The margin of this muscle has been dissected from the bony posterior choana. A circular muscle, whose margin was partially separated from the superior constrictor appeared to 'grip' the aryteno- epiglottideal tube. This circular muscle is the palato-pharyngeus (Hosokawa, 1950) and it had an anterior attachment to the vomer. The disposition of the superior constrictor and the palato-pharyngeus to the aryteno-epiglottideal tube in the lateral position is demonstrated in Fig. 14. We postulate that the superior constrictor in combination with the palato-pharyngeus may act inter alia to expel water from the choanal region. In Fig. 15 the laryngo-pharynx is shown in wider perspective and the palato- pharyngeus has been partially retracted. A large probe has been passed through the oro-pharynx. It traverses the pyriform fossa (which is beside the larynx) and enters the oesophagus. This further demonstrates the separation of the aero-digestive tracts in this odontocete.

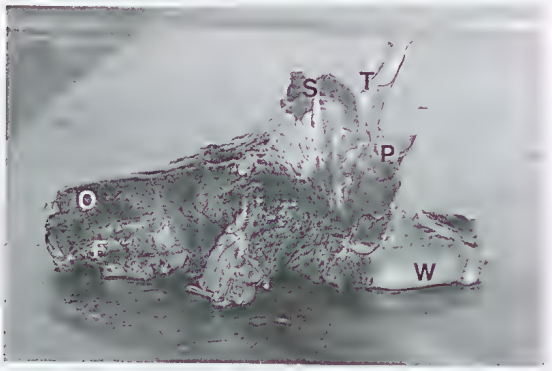

FIG. 14. Laryngo-pharynx *Mesoplodon densirostris* JM9640 from lateral aspect. (F) trachea; (O) oesophagus; (P) palato-pharyngeus; (S) superior constrictor; (T) aryteno-epiglottideal tube; (W) oro-pharynx.

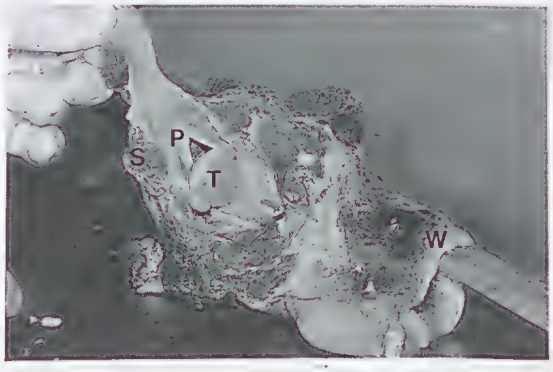

FIG. 15. Laryngo-pharynx *Mesoplodon densirostris* JM9640 from dorso-rostral aspect. The large probe is seen in the oro- pharynx. It was passed through the left pyriform fossa to enter the oesophagus which is obscured by the retracted superior constrictor and palato-pharyngeus. (P) palato-pharyngeus; (S) superior constrictor; (T) aryteno-epiglottideal tube; (W) oro-pharynx.

In this fresh specimen it was not possible to retract the aryteno-epiglottideal tube. Pilleri (1979) considered, on the basis of acoustic experiments, that the aryteno-epiglottideal tube was retracted during deglutition and disagreed with Rawitz (1900) who stated that food passed to the side of the larynx. Our opinion, based on morphological considerations, concurs with that of Rawitz.

ACKNOWLEDGEMENTS

We are indebted to many people who assisted with retrieval and preparation of the specimens. Alan Genninges of the Moreton Island Protection

Committee photographed JM8658 and Reg Lambert photographed JM8807. Brendan McLarty of QNPWS secured JM8658 and transported us to the stranding site. Lis Sedlak-Weinstein of the University of Queensland examined JM8807 for parasites and assisted with retrieval of the specimen. John Ford of QNPWS photographed JM9640 and secured the specimen. Paul Stumkat of the Queensland Museum retrieved its skeleton. John Musgrave of Sullivan, Nicolaides and Partners arranged the histological examination of JM8807 and Stephen Marmo of the X-ray Department, Royal Brisbane Hospital took the radiographs. Bruce and Carolyn Cowell patiently and skilfully photographed and prepared material at the Queensland Museum and Jeff Wright took some of the laryngeal photographs.

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BRACONINE WASPS OF AUSTRALIA

DONALD L. J. QUICKE AND SIMON N. INGRAM

Quicke, D.L.J. & Ingram, S. N. 1993 06 30: Braconine wasps of Australia. *Memoirs of the Queensland Museum* 33(1): 299-336. Brisbane. ISSN 0079-8835.

An illustrated key to the 45 genera of Braconinae known from Australia is provided. *Pycnobraconoides* gen.nov. (type species: *Ichneumon mutator* Fabricius) is described and illustrated. Thirteen new species are described and illustrated: *Acrocerilia tricolor* sp.nov. (Queensland); *Africadesha tobiasi* sp.nov. (Queensland); *Atanycolus australiensis* sp.nov. (Queensland); *Calcaribracon willani* sp.nov. (Queensland); *Furcadesha walteri* sp.nov. (Queensland); *Myosoma rufescens* sp.nov. (Queensland); *Pedinopleura australiensis* sp.nov. (Queensland); *Simplicibracon nigritarsus* sp.nov. (Queensland); *Testudobracon australicolorus* sp.nov. (Queensland); *Testudobracon tatyanae* sp.nov. (Queensland); *Testudobracon unicolorus* sp.nov. (Queensland); *Trigastrotheca tricolor* sp.nov. (Queensland) and *Virgulibracon endoxylaphagus* sp.nov. (Queensland). *Poecilobracon* Cameron is treated as junior synonym of *Callibracon* Ashmead. *Bracon froggatti* Cameron is transferred to *Pycnobraconoides* gen.nov. Nine genera are recorded from Australia for the first time: *Acrocerilia* van Achterberg; *Africadesha* Quicke, *Atanycolus* Foerster, *Furcadesha* Quicke, *Gelasinibracon* Quicke, *Paranesaulax* Quicke, *Rostraulax* Quicke, *Trigastrotheca* Cameron and *Vipiomorpha* Tobias. *Calcaribracon diores* (Cameron) is recorded from Australia for the first time. Notes are provided on the distributions and biologies (when known) of all the genera. □ *Hymenoptera, Braconidae, Braconinae, wasp, parasite, Australia, key, new genera, new species, synonymy.*

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The Braconinae is a huge, cosmopolitan subfamily of parasitic wasps with nearly 5000 described species (Shenefelt, 1978) distributed among more than 200 genera worldwide. The vast majority of species are ectoparasitoids principally on coleopterous and lepidopterous hosts though a few attack Diptera, Hymenoptera-Symphyta and possibly Homoptera and one group, the Aspidobraconina, are endoparasitic on butterfly pupae.

Only a minority of extant species have been described and there are also undoubtedly numerous new genera awaiting discovery, the Australian fauna of braconine wasps being particularly poorly known. The last generic key dealing specifically with Australia is that of Szépligeti (1906) which included 10 genera. More recently, Parrott (1953) catalogued the Australian Braconinae listing 12 genera compared with the 45 now known to occur there. More Australian species can be identified to genus with the key to the Old World genera provided by Quicke (1987b). However, since that time, several new Australian genera have been described (Quicke, 1988c, 1989d; Quicke & Tobias, 1990) and it is therefore thought that the presentation of an illustrated key to the Australian genera would be both timely and would encourage much needed investigation of Australian braconine wasp biology.

TERMINOLOGY AND COLLECTIONS

Terminology follows that of van Achterberg (1979, 1988). Wing veins are measured from the centres of their junctions (except for forewing vein r and where otherwise stated), length of head is measured perpendicular to the face (re: couplet 34), length of femur excludes trochantellus and ovipositor length refers to that part which would normally project beyond the apex of the metasoma when directed posteriorly as in most set specimens.

Abbreviations for museums are: American Entomological Institute, Gainesville (AEIG); Australian Museum, Sydney (AMSA); Australian National Insect Collection, Canberra (ANIC); Hungarian Natural History Museum, Budapest (HNHM); Natural History Museum, London (BMNH); Queensland Department of Primary Industries, Indooroopilly, Brisbane (QDPI); Queensland Museum, South Brisbane (QMBA); Quicke Collection, Sheffield (QC).

KEY TO THE GENERA AND SUBGENERA OF AUSTRALIAN BRACONINAE (♀♀ ONLY)

The following key is arranged so as to obtain reasonably quick identification of Australian genera and thus the first key character is chosen so as to divide the known genera into two, roughly equal-sized groups. By reference to Figures 27-35 the shape of the scapus of the great majority of specimens encountered should be unambiguously assignable to one category or the other. The few genera with species showing variation or intermediate conditions (notably in the Aphrastobraconina, viz *Cedilla*, *Curriea*, *Ligulibracon*, *Megalommum* and *Undabracon* and especially *Eucurriea*) are allowed for by a loop. To assist further with use of couplet 1, and to help allow for specimens in which both antennae are missing, a list of unique characters for genera and groups is provided in Table 1.

1. Scapus shorter ventrally than dorsally in lateral aspect when directed anteriorly, usually small (Figs 27, 28, 31, 47, 48, 75, 76, 81, 85), not emarginate medially (Fig. 47) and at most only weakly emarginate laterally (Figs 31, 47) (see Table 1 in case of uncertainty) 2
   - Scapus at least as long or longer ventrally than dorsally in lateral aspect when directed anteriorly, often cylindrical and large (Figs 32-35, 39, 44, 80), usually with well-developed apico-medial and apico-lateral emarginations 32
2. Forewing vein CU1a arising at the same level as 2-CU, vein CU1b much longer than 3CU-1 if the latter is distinct (Fig. 12) (Adeshini) 3
   - Forewing vein CU1a arising well below the level of 2-CU, vein 3CU-1 at least as long as and usually much longer than vein CU1b (Figs 13, 15-19, 94-100) 4
3. Posterior margin of 5th metasomal tergite strongly produced on either side of the midline (Figs 110, 111) ..... *Furcadesha*
   - Posterior margin of 5th metasomal tergite not produced sub- medially ..... *Africadesha*
4. First metasomal tergite fused to metasomal syntergite 2+3, the junction between tergites 1 and 2 being represented by a crenulate sulcus (Figs 74, 121) (Aspidobraconina) 5
   - First metasomal tergite movable joined to metasomal syntergite 2+3, there being a normal arthrodial intersegmental membrane between tergites 1 and 2 (Figs 59-71) 6
5. Median area of metanotum with a complete mid-longitudinal carina; dorsal carinae of 1st metasomal tergite running separately to posterior margin of tergite; base of hindwing with a glabrous area; median lobe of mesoscutum with a pair of submedial, longitudinal grooves anteriorly; 6th tergite with relatively shallow peri-basal, transverse groove (Fig. 121) ..... *Pedinopleura*
   - Median area of metanotum without a complete carina (Fig. 105); dorsal carinae of 1st metasomal tergite uniting mid-posteriorly well before posterior margin of tergite (Fig. 74); base of hindwing more or less evenly setose; median lobe of mesoscutum without sub-medial longitudinal grooves anteriorly; 6th tergite with deep peri-basal, transverse groove (Fig. 115) ..... *Hyboteles*
6. Propodeum with a complete, lamelliform mid-longitudinal carina (see Fig. 105) 7
   - Propodeum without a complete lamelliform mid-longitudinal carina or with only a short one posteriorly 12
7. Posterior margin of 6th metasomal tergite with a (usually) deep, narrow, semicircular, medial emargination (Figs 117, 118, 120) and (usually) tergites 3-5 distinctly roundly produced laterally (Figs 116, 119); metasomal syntergite 2+3 wider than long; ovipositor as long as or longer than the metasoma ..... *Testudobracon*
   - Posterior margin of 6th metasomal tergite not narrowly emarginate medially nor roundly produced laterally (Fig. 113); metasomal syntergite 2+3 longer than wide (Figs 71, 73); ovipositor usually shorter than half the metasoma 8
8. Posterior margin of 6th metasomal tergite with a pair of submedian emarginations leaving a sharp median prominence (Figs 112, 113) .*Trigastrotheca*

Character	State	Go to key couplet
Scapus	petiolate, strongly or angularly narrowed at base with concave basal profile (Fig 44)	40
Propodeum	with a complete, mid-longitudinal (usually lamelliform) carina (Fig 105)	2
Forewing vein 3-CU1	absent or much shorter than vein CU1b (Figs 12, 89)	3
Forewing veins CU1b	much wider than posterior part of vein 3CU1 (Figs 21, 22, 94)	32
Claws	bifurcate (Figs 57, 58)	42
Basal lobe of claw	pointed or with small accessory tooth (Figs 52-54)	2
1st metasomal tergite	fused immovably to 2nd (Fig 74)	5

TABLE 1. Characters characterizing and unique to genera or groups of genera and key couplet to proceed from to complete identification

- Posterior margin of 6th metasomal tergite without submedial emarginations nor with a median prominence 9

9. Base of hindwing with a large glabrous area distal to, and approximately the same size as, the subbasal cell; scutellum with a well-developed pit medio-anteriorly; forewing vein r-m with only a single posterior bulla; forewing 2nd submarginal cell virtually parallel-sided, veins 3-SR and 2-M not noticeably converging distally ....*Acrocerilia*

- Base of hindwing more or less evenly densely setose with at most only a small glabrous area around vein 2-1A; scutellum without a medio-anterior pit; forewing vein r-m variable but often with a distinct bulla and associated flexion line anteriorly as well as posteriorly; forewing 2nd submarginal cell narrowing distally 10

10. Hindwing vein 2-SC+R transverse (Fig. 102); ovipositor (part extending beyond apex of metasoma) longer than the median length of the 2nd metasomal tergite; transverse median clypeal carina strongly protruding (Fig. 76)..... ..... *Simplicibracon*

- Hindwing vein 2-SC+R longitudinal (Fig. 101); ovipositor (part extending beyond apex of metasoma) shorter than medial length of 2nd metasomal tergite; transverse median clypeal carina less strongly protruding 11

11. Precoxal suture represented by a deep, smooth, medial, circular pit; 2nd metasomal suture interrupted medially at least by a strong ridge, usually by a wider area (Figs 71, 73); median area of metanotum with a complete mid-longitudinal carina.....*Gelasinibracon*

- Precoxal suture represented by an elongate distinctly sculptured impression; 2nd metasomal suture not interrupted medially; median area of metanotum bulbous, without a complete mid-longitudinal carina .....*Esengoides*

12. Basal lobes of claws at least angularly narrowing before the claw (Figs 53, 54), sometimes produced into a distinct tooth-like process (Fig. 52) 13

- Basal lobe of claws smoothly curved (Figs 55-57) 20

13. Hindwing with at least a pigmented line representing vein 3- CU (Fig. 14; separated from remainder of venation); basal lobe of claws produced into a tooth-like process (Fig. 52) 14

- Hindwing without vein 3-CU (Figs 15-19); basal lobe of claws angularly narrowed, but not toothed (Figs 53, 54) 15

14. Labio-maxillary complex elongate; hindwing vein 2-SC+R strongly transverse (Fig. 14) ....*Calcaribracon* (*Calcaribracon*)

- Labio-maxillary complex normal; hindwing vein 2-SC+R interstitial or longitudinal (see Fig. 101) .....*Calcaribracon (Arostrobracon)*

15. Shortest distance between 1st discal cell and 2nd submarginal cell of forewing at least 0.85 times shortest distance between 1st submarginal and 3rd submarginal cell (Fig. 15) .....*Tropobracon*

- Shortest distance between 1st discal cell and 2nd submarginal cell not more than 0.7 times shortest distance between 1st and 3rd submarginal cells (Figs 16, 17, 87, 89) 16

16. Marginal cell of forewing short, vein SR1 reaching wing margin less than 0.65 times the distance between the apex of the pterostigma and the wing tip (Fig. 16); propodeum largely sculptured .....*Vipiomorpha*

- Marginal cell of forewing longer, vein SR1 reaching wing margin more than 0.8 times the distance between the apex of the pterostigma and the wingtip (Figs 17-19); propodeum often smooth 17

17. First metasomal tergite very slender, more than 3.0 times longer than maximally wide (Fig. 70); forewing vein 1-SR+M straight or virtually so; metasoma completely smooth and shiny .....*Myosoma*

- First metasomal tergite less than 2.5 times longer than maximally wide (see Figs 65-67); forewing vein 1-SR+M straight or curved; metasoma variably sculptured 18

18. Forewing vein 1-SR+M strongly curved posteriorly after arising from vein 1-SR (Fig. 17; see also Fig. 91); median flagellomeres shorter than wide; metasoma completely smooth and shin ....*Mollibracon*

- Forewing vein 1-SR+M straight or weakly curved (see Figs 12, 13) or if strongly curved (some *Bracon* spp.) then the median flagellomeres are distinctly longer than wide; metasoma variably sculptured 19

19. Forewing vein 3-SR more than 1.6 times longer than vein r, usually more than 1.9 times longer (see Figs 87, 88); forewing vein r more or less straight (see Fig. 88).....*Bracon* (part)

- Forewing vein 3-SR less than 1.5 times longer than vein r, usually less than 1.2 times (Fig. 86); forewing vein r usually rather sinuous (Fig. 86) .....*Habrobracon*

20. Middle of clypeus strongly produced to form a massive beak- like process (Figs 9, 10)..... .....*Psittacibracon*

- Middle of clypeus at most with a lamelliform carina (Fig. 75) 21

21. Forewing vein CU1b much wider anteriorly than posterior part of vein 3-CU1 (Figs 21, 22, 94), 1st subdiscal cell being more or less strongly ovoid

or petiolate (Figs 21, 22, 94) (Aphrastobraconina part) 33

- Forewing vein CU1b not or hardly wider than posterior part of vein 3-CU1 (Figs 95-100), 1st subdiscal cell not ovoid or petiolate 22

22. Pedicellus large, highly petiolate, medially protruding and with a large but discrete patch of specialized sensillae (Fig. 85); fore tibia with a longitudinal row of thickened, peg-like setae (Fig. 83) .....*Serratobracon*

- Pedicellus normal-sized, not petiolate and without a patch of specialised sensillae (if with sensillae then these not restricted to one side of pedicellus) (see Figs 27, 28, 31); fore tibia without a longitudinal row of thickened, peg-like setae 23

23. With a strong spur arising from forewing vein 3-CU1 (Fig. 100); transverse median clypeal carina strongly protruding (Fig. 75); forewing vein 1-SR+M moderately curved, not sharply angled (see Figs 21, 26) .....*Ploceibracon*

- Forewing vein 3-CU1 usually without a spur (see Figs 96-99) or if with a spur (e.g. some *Virgulibracon*) then transverse median clypeal carina not strongly produced (see Figs 44-48) and/or forewing vein 1-SR+M sharply angled (Figs 90, 92) 24

24. Ovipositor without a pre-apical dorsal notch or nodus (Figs 128, 130, 131) 25

- Ovipositor with a distinct pre-apical dorsal notch or nodus (see Figs 133-138) 27

25. Ovipositor very short, thick and laterally compressed (Fig. 131), the exserted part shorter than metasomal syntergite 2+3; all metasomal tergites largely smooth and shiny .....*Stigmatobracon*

- Ovipositor longer and more slender (Figs 128, 130), the exserted part longer than metasomal syntergite 2+3; at least basal 2 metasomal tergites largely coarsely sculptured (Fig. 67) 26

26. First metasomal tergite with a well-developed mid-longitudinal carina (Fig. 67); ovipositor gradually and more or less evenly narrowing from base to apex (Fig. 128); eyes virtually glabrous .....*Hybogaster*

- First metasomal tergite without a mid-longitudinal carina; ovipositor distinctly deepening pre-apically (Fig. 130); eyes usually setose..... .....*Pycnobraconoides* gen.nov.

27. Forewing vein 1-SR+M sharply and strongly angled posteriorly approximately one third of the distance from its base (Figs 19, 90, 92), often with a distinct spur arising from the angulation (Fig. 92) 28

- Forewing vein 1-SR+M straight or gently and more or less evenly curved posteriorly (see Figs 87, 91, 94, 97), without a spur 30

28. First metasomal tergite with dorsal carina joining dorso-lateral carina (Figs 66, 108); second metasomal tergite with a large well-developed mid-basal, posteriorly narrowing, triangular area (Fig. 66); 3rd metasomal tergite with well-developed antero-lateral, posteriorly diverging grooves; hindwing with a glabrous area distal to vein 1r-m .....*Vomeribracon*

- First metasomal tergite without dorsal or dorso-lateral carinae (Fig. 65); second metasomal tergite without a posteriorly narrowing, mid-basal triangular area, sometimes with a pair of posteriorly diverging grooves (Fig. 65); 3rd metasomal tergite without, or with only weak, antero-lateral grooves 29

29. Forewing vein r-m with only one bulla (posterior one); antero-lateral areas of 2nd metasomal tergite membranous, unsclerotized ... *Virgulibracon*

- Forewing vein r-m with two bullae; antero-lateral areas of 2nd metasomal tergite distinctly sclerotized .....*Virgulibraconoides*

30. Forewing cu-a interstitial or virtually so (see Figs 97-100); lower part of clypeus sharply recessed into the hypoclypeal depression (see Figs 41-43, 47); ovipositor less than 2.5 times longer than forewing; forewing veins C+SC+R and 1-SR forming an angle of more than 50°; base of hindwing usually evenly setose .....*Bracon* (part)

- Forewing vein cu-a postfurcal, removed from vein 1-M by more than the width of a vein (Figs 20, 96); lower part of clypeus hardly recessed into hypoclypeal depression, the hypoclypeal hair brushes orientated more or less anteriorly (Fig. 48); ovipositor more than 3.5 times longer than the forewing; forewing veins C+SC+R and 1-SR forming an angle of less than 50°; base of hindwing with a large glabrous area 31

31. Hindwing vein 1r-m longer than vein SC+R1 (Fig. 20) .....*Euurobracon*

- Hindwing vein 1r-m shorter than SC+R1 (see Figs 101, 102) .....*Euurobraconoides*

32. Forewing vein 3-CU1 (usually) narrowing posteriorly where it is narrower than the anteriorly thickened vein CU1b (Figs 21, 22, 94); 1st subdiscal cell with a medio-distal glabrous area (Figs 21, 22, 25); forewing vein 2-1A often markedly curved or angled (Fig. 94) (Aphrastobraconina) 33

- Forewing vein 3-CU1 not markedly narrowed posteriorly and not narrower than vein CU1b (Figs 97-99); 1st subdiscal cell usually evenly setose; forewing vein 2-1A not strongly curved or angled (see Figs 97-99) 39

33. Ovipositor formed into 3 arch-like sections poste-

riorly (Fig. 125); base of hindwing evenly setose ..... *Undabracon*

- Ovipositor at most formed into a single distal arch (Figs 123, 124, 126); base of hindwing with a large glabrous area 34

34. Ovipositor formed into a single distal arch (Figs 123, 124); fore wing vein r-m with a single posterior bulla (Figs 21, 88) 35

- Ovipositor not formed into an arch distally (Fig. 126); forewing vein r-m with two bulli (see Fig. 20) or largely unsclerotized (Fig. 22) 36

35. Ovipositor arch shallow, occupying approximately 0.3 of the exerted length of the ovipositor, base of arch indicated by angular expansion of the lower valves (Fig. 123); labio-maxillary complex somewhat elongate ..... *Ligulibracon*

- Ovipositor arch deep, occupying less than 0.2 of the exerted length of the ovipositor, without angular basal projections of the lower valves (Fig. 124); labio-maxillary complex not elongate ..... *Cedilla*

36. Width of head (across eyes)/length of head less than 1.48 ; face with coarse foveate to rugose sculpture (Fig. 41) 37

- Width of head (across eyes)/length of head more than 1.50; face shiny, smooth with scattered punctures (Fig. 43) ..... *Eucurriea*

37. Length of forewing vein 3-SR less than 1.65 times length of m-cu (Fig. 25); 1st tergite with weak dorso-lateral carinae ..... *Vipiellus* (part)

- Length of forewing vein 3-SR more than 1.7 times length of m-cu (Fig. 22); 1st tergite with or without dorso-lateral carinae 38

38. First metasomal tergite without dorso-lateral carinae (Fig. 61) ..... *Megalommum*

- First metasomal tergite with at least a trace of dorso-lateral carinae (see Figs 60, 66, 67) ..... *Curriea*

39. Scapus angularly narrowed basally (petiolate), with a broad preapical concave ledge (Figs 34-36, 39, 80); only ever with one specialized bristle at apex of hindwing vein C+SC+R (Figs 51, 103); pedicellus petiolate, strongly protruding medially with area of specialized sculpture (Figs 34, 35, 37, 38, 80) 40

- Scapus not angularly narrowed basally, without such a broad preapical ledge (Figs 29, 32); often with more than one especially thickened seta at apex of hind wing vein C+SC+R (Figs 49, 50); pedicellus more or less parallel-sided or distally narrowing, at most only slightly narrowed basally, not produced medially (Figs 29, 32, 33) 42

40. Face with a well-developed, transverse, protruding plate (Figs 39, 40, 44); apico-ventral setae of penultimate tarsal article very long, more than 0.8 times ventral length of telotarsus 41

- Face without a plate-like projection (Fig. 77); apico-ventral setae of penultimate tarsal articles much shorter, not more than 0.5 times ventral length of telotarsus (see Figs 53, 55) .. *Atanycolus*

41. Face with a horn-like, apically truncate projection medially arising from the base of the plate-like projection (Fig. 40) ..... *Chaoilta (Blastomorpha)*

- Face at most with a mid-longitudinal, lamelliform carina above the plate-like projection (Fig. 39) ..... *Chaoilta (Chaoilta)*

42. Claws bifurcate (Figs 57, 58) ..... *Macrobracon*

- Claws simple (Figs 55, 56) 43

43. Length of 1st subdiscal cell (parallel to vein 2-CU1) more than twice width of cell (perpendicular to vein 2-CU1) (Figs 23, 97); forewing vein r-m short, almost entirely unsclerotized, not tubular, without distinct bullae (Fig. 23); ovipositor with at least a weak pre-apical dorsal notch or nodus (Figs 135, 136) ..... *Eunesaulax*

- 1st subdiscal cell less than 1.9 times longer than wide (Fig. 25) or if shorter then either forewing vein r-m longer, largely sclerotized and tubular, often with 1 or 2 distinct bullae (see Figs 20-22, 24-26), or ovipositor without a pre-apical dorsal notch or nodus (Figs 127-132) 44

44. Forewing vein 1-SR+M distinctly curving towards the anterior wing margin after arising from 1-SR (Fig. 93; see also Fig. 16); angle between veins 1-SR and C+SC+R less than 50°; forewing vein r more than 0.69 times length of m-cu ..... *Stenobracon*

- Forewing vein 1-SR+M usually distinctly curved posteriorly after arising from 1-SR (see Figs 19-26, 90, 97) or if more or less straight then angle between veins 1-SR and C+SC+R more than 55°C and/or vein r less than 0.65 times length of vein m-cu 45

45. Ovipositor (part extending beyond apex of metasoma) more than twice length of forewing 46

- Ovipositor (part extending beyond apex of metasoma) less than 1.4 times length of forewing 47

46. Apex of ovipositor smoothly expanded but without a pre-apical dorsal nodus or apicoventral serrations (Fig. 127); 2nd metasomal tergite smooth (Fig. 106); 3rd metasomal tergite with a medially broken, transverse median groove or a pair of broader depressions (Fig. 106), otherwise smooth and shiny; labio-maxillary complex not elongate; posterior margin of propodeum simple, without carinae ..... *Paranesaulax*

- Apex of ovipositor with a distinct pre-apical dorsal nodus and ventral serrations; 2nd metasomal tergite coarsely sculptured (Fig. 104); 3rd metaso-

mal tergite without a transverse median groove, largely sculptured; labio-maxillary complex moderately elongate; posterior margin of propodeum with one or more pairs of short, anteriorly diverging carinae ..... *Rostraulax*

47. Ovipositor without a pre-apical dorsal notch or nodus (Fig. 129, also see Fig. 128) 48
- Ovipositor with a pre-apical dorsal notch or nodus (see Figs 133, 134) 49

48. 2nd metasomal tergite with a posteriorly narrowing, mid-basal raised triangular area (see Fig. 60); forewing vein 3-SR less than 1.9 times length of r-m (Fig. 25); posterior margins of metasomal tergites 3-5 membranous, without transverse subposterior grooves ..... *Vipiellus* (part)
- 2nd metasomal tergite without a posteriorly narrowing, mid- basal triangular area (Fig. 63); forewing vein 3-SR more than twice length of r-m; posterior margins of metasomal tergites 3-5 sclerotized and convex in lateral profile .and with transverse subposterior groove ..... *Iphiaulax*

49. Metasoma short, robust and strongly sculptured (Fig. 62); 3rd metasomal tergite more than 3.75 times wider than minimally long. *Campyloneurus*
- Metasoma moderately elongate and largely smooth and shiny (Fig. 64); 3rd metasomal tergite less than 2.25 times wider than minimally long ..... *Callibracon*

NOTES ON THE AUSTRALIAN GENERA INCLUDING DESCRIPTIONS OF A NEW GENUS AND NEW SPECIES

New records for genera occurring in Australia are indicated by an asterix. Full details of synonymy are given in Shenefelt (1978), Quicke (1987b, 1991a) and Quicke & van Achterberg (1990).

*Acrocerilia van Achterberg

Previously known only from the type species, *A. pachynervis* van Achterberg, from the Philippines where it has been reared from the gracillariid cocoa moth, *Acrocercops cramerella* Snellen. The biological details available for this species indicate that it emerges from the prepupa of its host and therefore van Achterberg (1989) cautiously suggested that it might in fact be an endoparasitoid though precise data are lacking. In terms of its relationships, *Acrocerilia* appears intermediate in structure between certain genera of the *Plesiobracon* group, in particular *Psilolobus* van Achterberg and *Simplicibracon* Quicke, and members of the Aspidobraconina (see *Hyboteles* van Achterberg and *Pedinopleura* van Achterberg). If an association with the Aspidobraconina which are endoparasitoids of butterfly pupae is proven then this would add some support to the possibility that *Acrocerilia* might also be endoparasitic.

Key to species of *Acrocerilia*

1. Top of head coriaceous; head black and white; metasoma dorsally black with a white margin; hindwing vein 1-M narrowing distally..... ..... *A. tricolor* sp.nov.
- Top of head smooth; head brownish yellow; metasoma entirely brownish yellow; hindwing vein 1-M uniformly broad along its whole length .... *A. pachynervis* van Achterberg

Acrocerilia tricolor sp.nov.

MATERIAL EXAMINED

HOLOTYPE: ♂ labelled: 'AUSTRALIA NE Queensland Conway Range Nat. Park E from Proserpine' and 'No. 226, 22.II.1981 leg. Hangay and Vojnits at light'. Deposited in QMBA.

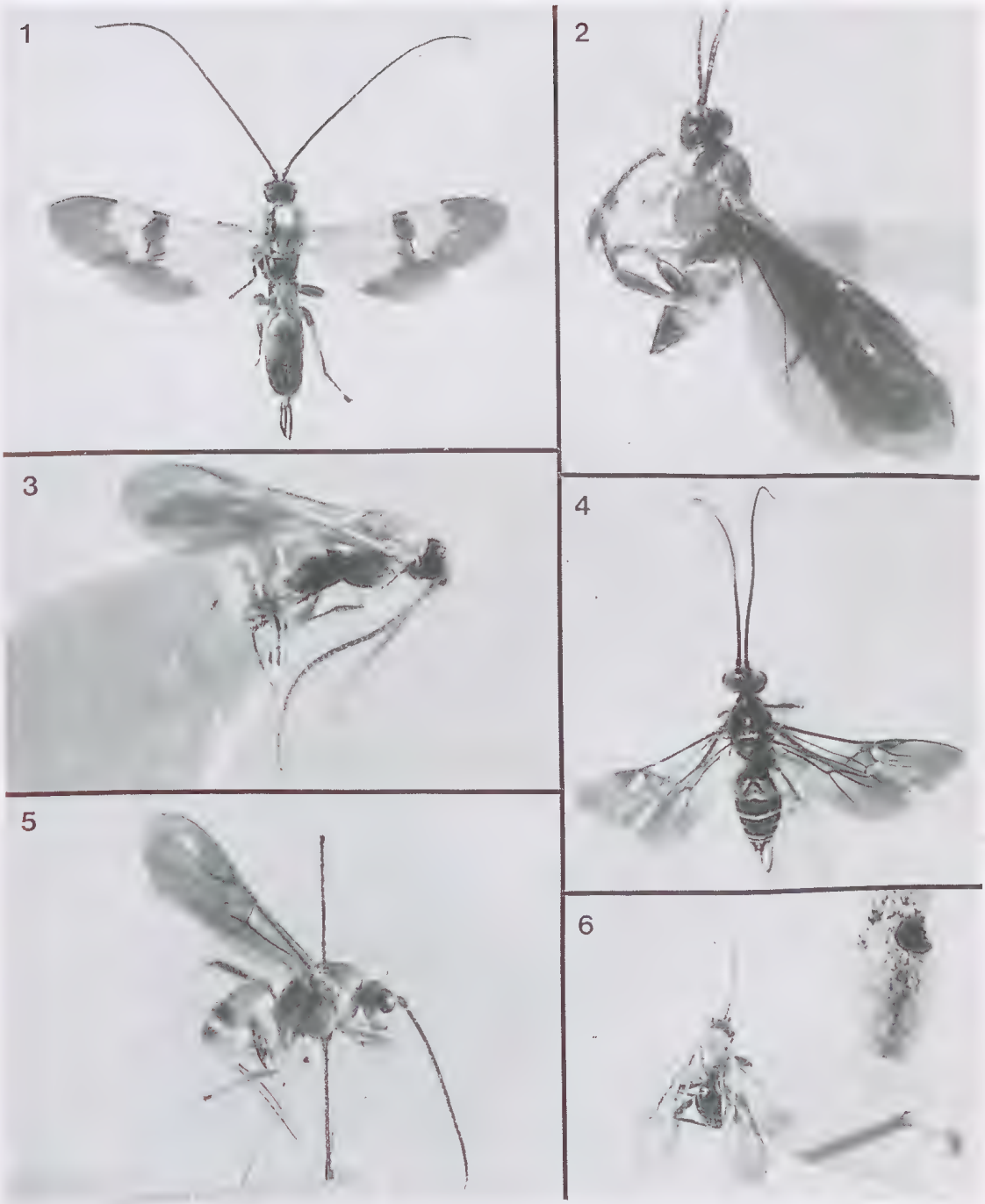
PARATYPE: ♂ labelled: 'AUSTRALIA NE Queensland Conway Range Nat. Park E from Proserpine' and '18.II.1981 No. 177 leg. Hangay and Vojnits, at light'. HNHM.

DESCRIPTION (♂♂)

Length of body 4.4-5.0mm, of forewing 4.0-4.5mm and of antenna 4.6-5.0mm.

Antennae with 43-44 flagellomeres. Terminal flagellomere acuminate. First flagellomere 1.07 and 1.15 times longer than the 2nd and 3rd respectively, the latter being 1.5 times longer than wide. Height of clypeus: inter-tentorial distance: tentorio- ocular distance = 1.0: 3.8: 2.9. Height of eye: shortest distance between eyes: width of head = 1.0:1.29:2.37. Width of face: height of face = 2.05:1.0. Face except for supra clypeal triangle densely, finely punctate, the punctures being arranged in transverse rows giving the face a striate appearance. Eyes virtually glabrous. Frons, temples and occiput coriaceous, back of head becoming finely striate. Shortest distance between posterior ocelli: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.25:1.0:2.25. Horizontal length of eye: horizontal length of head behind eye = 2.85: 1.0.

Mesosoma 1.48 times longer than maximally high. Pronotum with crenulate groove laterally. Notauli moderately well-developed on anterior



FIGS 1-6. 1. *Stigmatobracon diversipennis* Turner, ♀. 2. *Myosoma rufescens* sp.nov., ♂ paratype. 3. *Trigastrotheca tricolor* sp.nov., ♀ paratype. 4. *Virgulibraconoides* sp., ♀. 5. *Simplicibracon nigritarsus* .sp.nov., ♀ holotype. 6. *Pycnobraconoides mutator* (Fabricius) comb. nov., ♀ and host cocoon with parasitoid's emergence hole.

half of mesoscutum, absent on posterior half. Scutellar sulcus with 5 transverse crenulae. Mesoscutum, scutellum, mesopleuron and mesosternum densely and evenly setose, punctulate. Precoxal suture indicated by a weak depression. Mesopleural suture punctate. Median area of metanotum with a short carina anteriorly; merging with a flat triangular plate posteriorly in one specimen. Propodeum with a complete mid-longitudinal carina bordered by crenulae; posterior margin with numerous strong crenulations merging into rugose sculpture on the posterior half of the propodeum.

Forewing. Pterostigma 2.8 times longer than maximally wide, Lengths of veins SR1: 3-SR:r = 5.0: 1.6: 1.0. Lengths of veins 2- SR:3-SR:r-m = 1.36:1.36:1.0. Vein 2-M curved. Vein 1-M straight. Vein 1-SR forming an angle of approximately 80°. Veins cu-a more or less interstitial.

Hindwing. Vein 1r-m 0.35 times length of SC+R1. Apex of C+SC+R with one especially thickened bristle. Vein 2-1A absent. Base of discal + subdiscal cell with a large glabrous area.

Lengths of fore femur: tibia: tarsus = 1.0: 1.13: 1.20. Lengths of hind femur: tibia: basitarsus = 2.0: 2.7: 1.0. Hind tibia slender, maximally deep at apex. Hind basitarsus 5 times long than deep.

Metasomal tergites 1-5 largely foveate-rugose. Second tergite 2.0 times wider than medially long. Second suture crenulate, moderately curved. Tergites 3-5 with well-developed, antero-lateral areas. Posterior margin of 5th tergite slightly irregular.

Head ivory-white except for tips of mandibles, a triangular mark above the clypeus and the frons, temples, occiput and back of head down to level of base of eye which are black. Mesosoma brownish orange except for propodeum which is largely piceous. Fore and middle legs brownish orange, hind legs piceous to black. Metasomal tergites black except for the following which are ivory-white: the base and lateral margins (broadly) of the 1st tergite, the lateral margins of tergites 1-5 (narrowly) and their antero-lateral triangular areas, and the posterior margin of the 5th tergite. Wings uniformly very pale brown with dark brown pterostigma and venation.

*Africadesha Quicke

Members of the Adeshini, these small wasps have wing lengths less than 3mm. *Africadesha* is previously known from a single Afrotropical species, *A. usherwoodi* Quicke, though several other undescribed Afrotropical species have been seen by the senior author. Despite the strange disjunct distribution indicated by the discovery of the new Australian species, the two species differ only in relatively small characters and there is no reason to doubt the two as being anything other than congeneric. Nothing is known of the biology of any of the Adeshini. Further, given their small size, it is quite likely that members of other genera of this tribe will be found in Australia and the reader is referred to van Achterberg (1983a) and Quicke (1986b, 1988f).

Key to species of *Africadesha*

1. First metasomal tergite more than 1.5 times longer than posteriorly wide; third metasomal tergite with well-developed longitudinally striate sculpture (Fig. 109) ..... *A. tobiasi* sp.nov.
- First metasomal tergite less than 1.4 times longer than posteriorly wide; third metasomal tergite without longitudinally striate sculpture ..... *A. usherwoodi* Quicke

Africadesha tobiasi sp.nov.
(Figs 12, 109, 134)

MATERIAL EXAMINED

HOLOTYPE: ♀ labelled: '15 km NE Kuranda, Queensland, 1.V-14.VI. 1985 MDPI FIT site 25, Storey & Halfpapp'. Deposited in QMBA.

PARATYPES: 3♀♀, same data as holotype. QMBA, QDPI and BMNH.

DESCRIPTION (♀♀)

Length of body 2.7mm, of forewing 2.6mm, of ovipositor (part exserted beyond apex of metasoma) 0.45mm and of antenna 4.2mm.

Antenna with 42 flagellomeres, considerably longer than the body. Terminal flagellomere pointed but not acuminate, 2.3 times longer than wide. Median flagellomeres 1.7 times longer than wide. First flagellomere 1.17 and 1.4 times longer than the 2nd and 3rd flagellomeres respectively, the latter being 2.25 times longer than wide. Height of clypeus: inter-tentorial distance: tentorio- ocular distance = 1.0:2.8:2.2. Face, frons and occiput coriaceous. Height of eye: shortest distance between eyes: width of head = 1.0:1.375:2.5. Shortest distance between posterior ocelli: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.5:1.0:3.5.

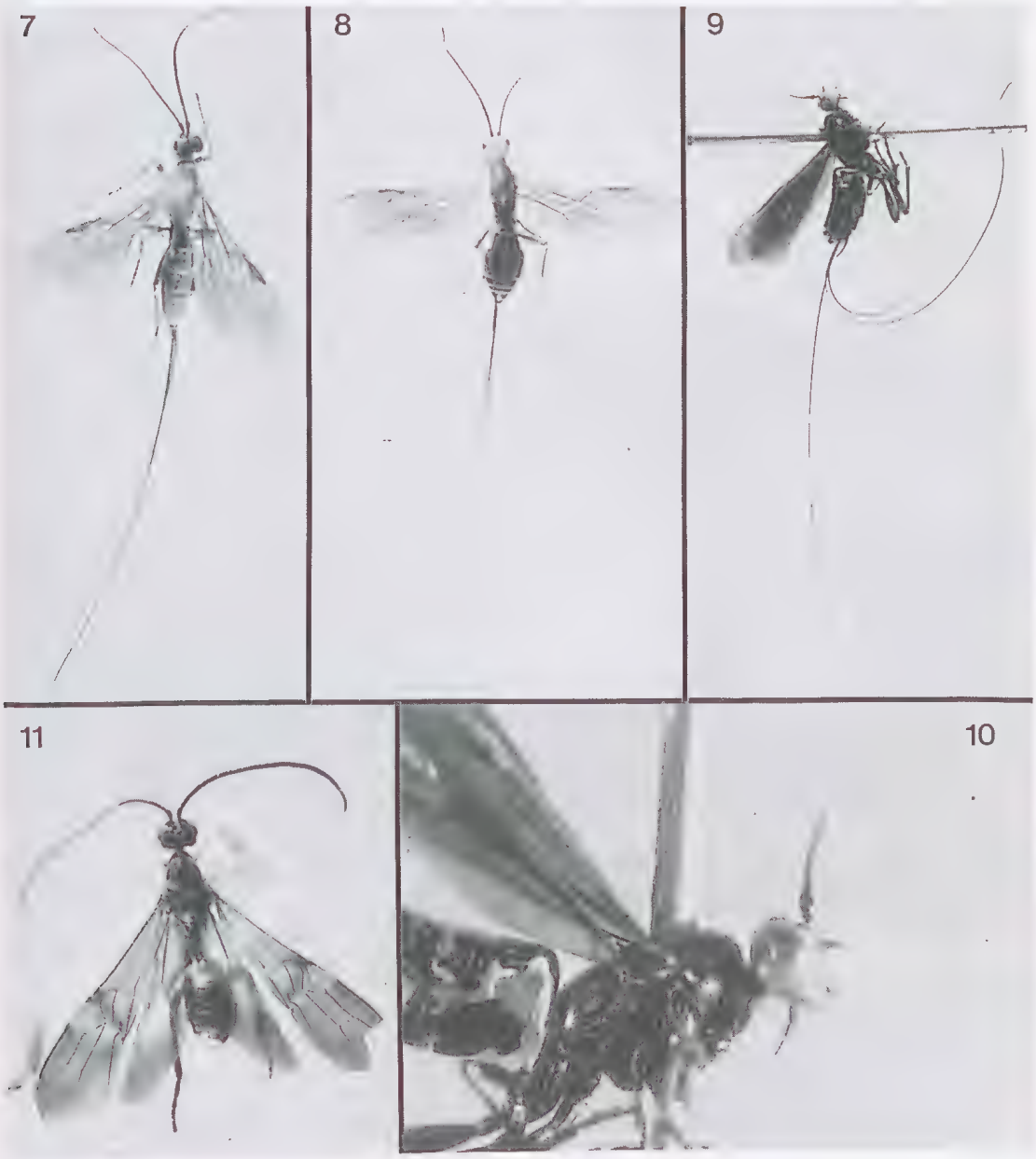
Mesosoma 1.5 times longer than high; largely coriaceous but mesosternum largely smooth and shiny. Precoxal suture very weakly, broadly im-

pressed. Mesopleural suture smooth. Propodeum with a complete mid-longitudinal carina.

Forewing. Lengths of veins SR1: 3-SR:r = 6.7:2.2:1.0. Lengths of veins 2-SR:3-SR:r-m = 1.7:2.0:1.0. Vein 2-SR+M moderately long; shortest distance between 1st subdiscal cell and 2nd submarginal cell: length of vein m-cu = 1.0: 1.25. Veins cu-a and 3-CU1 both more or less interstitial.

Lengths of fore femur: tibia: tarsus = 1.0: 1.2: 1.53. Lengths of hind femur: tibia: basitarsus = 1.47: 2.3: 1.0. Hind basitarsus 10 times long than deep.

First tergite 1.8 times longer than posteriorly wide; with rugose sculpture and with thin irregular mid-longitudinal carina. Second tergite 1.2 times wider posteriorly than medially long. Second and 3rd tergites with strong longitudinal



FIGS 7-11. 7. *Eunesaulax terebratus* Tobias, ♀. 8. *Euurobraconoides longicaudis* Quicke, ♀. 9,10. *Psittacibracon lacteolus* Quicke, ♀. 11. *Calcaribracon willani* sp.nov., ♀ holotype.

striations (Fig. 109) interspersed with punctate sculpture. Tergites 4 and 5 with fine rugulose to coriaceous sculpture. Fifth tergite without postero- lateral emarginations. Ovipositor (exserted part) about as long as the 5th tergite; with a distinct pre-apical dorsal nodus, apico-ventrally virtually smooth (Fig. 134).

Uniformly pale brownish yellow, flagellum becoming piceous beyond middle, ovipositor sheaths black. Wings weakly infuscate with brown venation.

ETYMOLOGY

Named after our esteemed colleague Vladimir Tobias of the Russian Academy of Science, St Petersburg, who drew our attention to many interesting Australian Braconinae.

*Atanycolus Foerster
(Figs 77, 80, 82, 84, 103)

Synonyms. Coelobracon Thomson; *Melanobracon* Ashmead; *Atanycolidae* Viereck.

A widespread genus of medium-sized wasps, commonest in the Nearctic and Palaearctic though with some closely related and more derived groups occurring in the neotropics (e.g. *Hemibracon* Szépligeti) and Indo-Australian region (*Nedinoschiza* Cameron). *Nedinoschiza*, which is probably only a specialized derivative of *Atanycolus*, has not yet been recorded from Australia though it may occur there; it can be distinguished from *Atanycolus* by the greatly enlarged anterior tentorial pits. (Quicke, 1987 b)

Atanycolus tomentosus Szépligeti, previously placed in the Braconinae (see Parrott, 1953), is in fact a member of the Doryctinae (Quicke, 1984).

Atanycolus australiensis sp.nov.
(Figs 77, 80, 82, 84)

MATERIAL EXAMINED

HOLOTYPE: ♀ with the following label: 'Australia 35-40 km NO Deniliquin, Tobias 12-13.iv.978'. Deposited in ANIC.

DESCRIPTION (♀)

Length of body 3.9mm, of forewing 3.8mm, of ovipositor (part exserted beyond apex of metasoma) 3.3mm and of antenna 3.0mm.

Antennae (broken) with at least 29 flagellomeres, all flagellomeres longer than wide. First flagellomere 1.25 and 1.5 times longer than 16 2nd and 3rd respectively, the latter being 1.75 times longer than apically wide. Height of eye: shortest distance between eyes: width of head = 1.1: 1.0:2.1. Face shiny, weakly at and with many deep punctures at the bases of the silvery setae. Eyes sparsely setose; emarginate opposite antennal sockets. Head very elongate (Fig. 77); length of head behind eye: horizontal length of eye = 1.0:1.0. Ocelli small; distance between posterior ocelli; transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 2.0: 1.0: 4.0.

Mesosoma 2.0 times longer than maximally high. Antescutal depression well-developed. Scutellar sulcus shallow with few weak punctures. Scutellum protruding in profile.

Forewing. Lengths of veins SR1: 3-SR: r = 5.3: 2.85: 1.0. Lengths of veins 2-SR: 3-SR: r-m = 1.56: 2.5: 1.0. Vein r-m largely unsclerotized. Vein 1-SR+M rather strongly curved. Veins C+SC+R and 1-SR forming an angle of approximately 80°. Vein cu-a interstitial. Vein CU1b almost as long as 3-CU1.

Hindwing. Vein C+SC+R very thick, apex with a single, very large, specialized catch bristle (Fig. 103). Base of wing evenly setose.

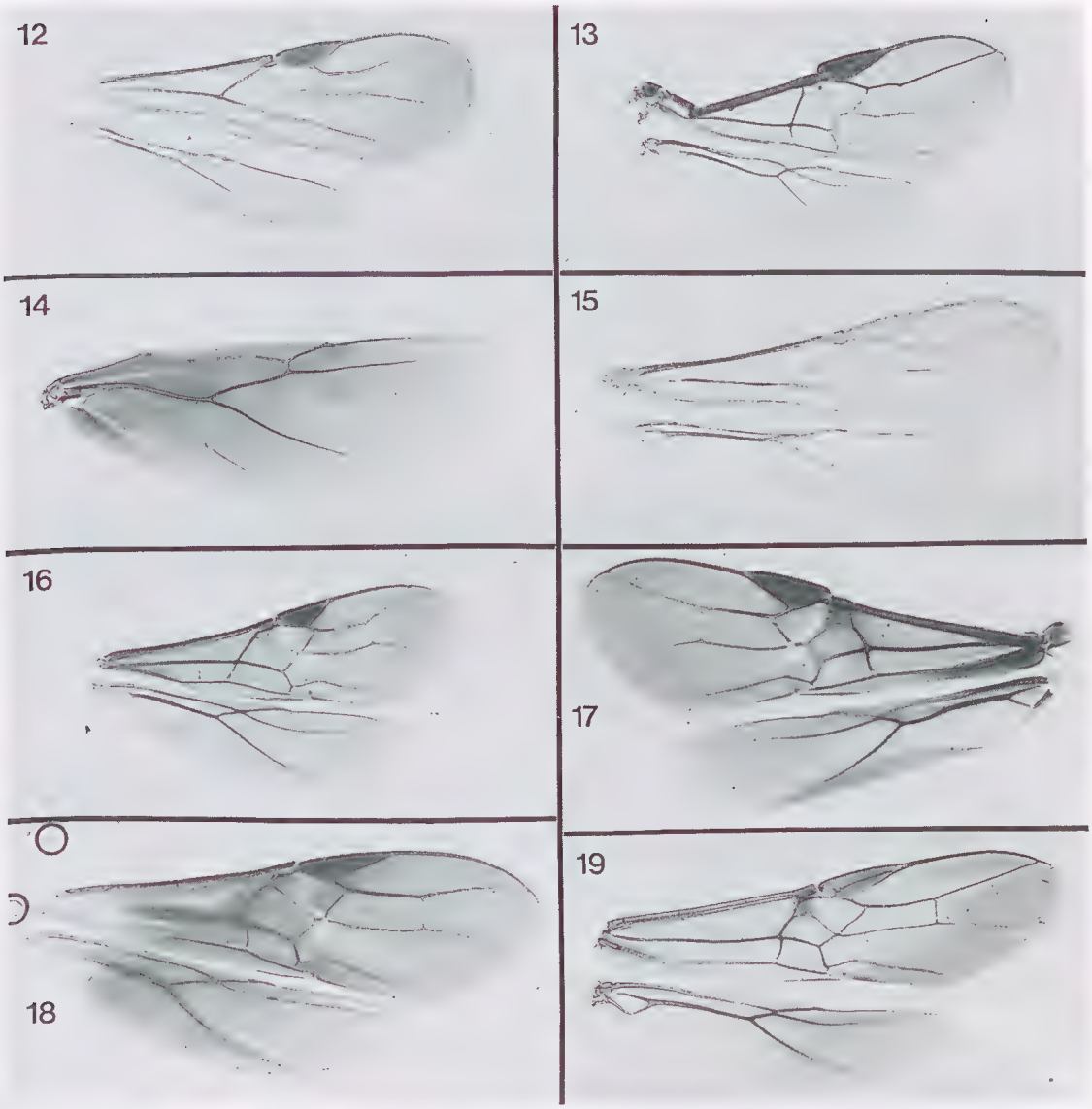
Fore tibia with a well-developed longitudinal row of pegs (Fig. 82), Length of fore femur: tibia: tarsus = 1.0: 1.16: 1.45. Length of hind femur: tibia: basitarsus = 1.95: 2.9: 1.0.

Metasoma largely smooth and shiny. First tergite more or less parallel-sided; raised median area with weak irregular, longitudinal striate sculpture. Second tergite 1.62 times wider than medially long; with a large, acute, triangular mid-basal area bordered on each side by a finely crenulate groove; with sub- lateral, curved, longitudinal, finely crenulate grooves. Second suture sinuous, crenulate. Third tergite with well developed antero-lateral areas. Tergites 3-6 smooth and shiny, without transverse sub-posterior grooves, with posterior margins membranous. Ovipositor (exserted part) approximately 0.85 times length of forewing.

Largely piceous brown except following: head orange-yellow; mesosoma and tergites 5-7, black; posterior (membranous) margins of tergites 4-6 ivory white. Wings light brown with darker brown venation.

Bracon Fabricius
(Figs 51, 53)

Synonyms. Microbracon Ashmead; *Amicoplidea* Ashmead; *Macrodyctium* Ashmead; *Tropidobracon* Ashmead; *Liobracon* (Ashmead) Nason; *Seliodus* Brethes.



FIGS 12-19. Wings: 12, *Africadesha tobiasi* sp.nov., ♀ paratype; 13, *Trigastrotheca* sp., ♀ (African species); 14, *Calcaribracon (Calcaribracon) diores* (Cameron); 15, *Tropobracon* sp., ♀ (African species); 16, *Vipiomorpha ypsilon* Tobias, ♀ (Russian specimen); 17, *Mollibracon bimaris* (Turner), ♀; 18, *Hybogaster* sp., ♀ (Papua New Guinea specimen); 19, *Virgulibracon endoxylaphagus* sp.nov., ♀.

A vast cosmopolitan genus of small wasps which parasitize a wide range of other insects (Quicke, 1988b). Concealed Lepidoptera larvae are the commonest hosts followed by Coleoptera, Diptera, and Hymenoptera-Symphyta (e.g. Austin & Faulds, 1989); in Australia, gall forming Homoptera also appear to be attacked (Chadwick & Nikitin, 1975) but this record should be checked by careful observation of larval feeding habits. To date only approximately twenty species have been recorded from Australia (Parrot, 1953; Austin & Faulds 1989). However, this is a considerable underestimate and the true number of Australian species is probably in the hundreds. The genus occurs throughout Australia and is morphologically rather diverse there with some distinctive species groups.

Calcaribracon Quicke
(Figs 11, 14, 27, 52, 91, 95)

A small genus ranging from Queensland through New Guinea, Indonesia and Malaysia to SE China and Japan. Keys to the species have been provided by Quicke (1986a, 1988d). Three species are known from Australia, all from Queensland, viz. *C.* (*Arostrobracon*) *walkeralis* (Shenefelt), *C.* (*Arostrobracon*) *diores* (Cameron) and *C.* (*Arostrobracon*) *willani* sp.nov. The Australian specimen of *C. diores* examined differs from the New Guinea specimens in the colour of the hind coxa and femur (yellow not black) and in having forewing vein cu-a less strongly curved. Thus it may in future be found to represent a further new species. We have also included the nominal subgenus in the generic key presented here though all known members of that group have a more northerly distribution (Papua New Guinea to China and Japan). Nothing is known of the biology of the Australian members of this genus but one Japanese species has been reared from larvae of members of the sesiid moth genus *Paranthrene* (Maetô, 1992), while a specimen of *C. ferax* (Smith) from Papua New Guinea in the BMNH has a label 'reared ex cerambycid larva' (Quicke, 1986a); while the former record is definitely correct and agrees better with the known hosts of the related genus *Myosoma* (Quicke, 1989c), the latter record could be erroneous.

Key to Australian species of *Calcaribracon*

1. Pterostigma, base of forewing vein r (usually), and 2nd metasomal tergite largely yellow or orange-yellow (Fig. 11); basal fifth to half of forewing yellow (Fig. 11) 2
   - Pterostigma, forewing vein r and 2nd metasomal tergite entirely piceous brown or black; forewing uniformly dark brown ..... *C. diores* (Cameron)
2. Propleuron, propodeum, mid-legs, hind femur, median area of 1st metasomal tergite, metasomal tergites 3-7 piceous or black (Fig. 11); basal half of forewing yellow ..... *C. willani* sp.nov.
   - Mesosoma and metasoma up to the 7th tergite, midlegs and hind leg except apex of tibia and tarsus, yellow or orange-yellow; forewing with only basal half of basal and sub-basal cells yellow ..... *C. walkeralis* (Shenefelt)

Calcaribracon (Arostrobracon) willani sp.nov. (Figs 11, 52, 91)

Material Examined
Holotype: ♀ with the following label: 'Zillmere Brisbane, Q. 27 August 1988 G.V. Maynard'. Deposited in QMBA.

Description (♀)
Length of body 8.3mm, of forewing 8.8mm, of ovipositor (part exserted beyond apex of metasoma) 1.1mm and of antenna 8.0mm.

Antenna with 65 flagellomeres. Terminal flagellomere acuminate, 1-8 times longer than maximally wide. Penultimate flagellomere 1.25 times longer than wide. Median part of flagellum rather flattened, median flagellomeres at their widest approximately 1.6 times wider than long. First flagellomere 1.7 times longer than both the 2nd and 3rd separately, the latter being 1.2 times wider than long. Height of eye: width of face: width of head = 1.1:1.0:2.0. Eyes sparsely setose. Lateral half of frons moderately densely with short erect setae. Horizontal length of head behind eye: horizontal length of eye = 1.0:1.37.

Mesosoma 1.7 times longer than high. Mesoscutum almost totally glabrous.

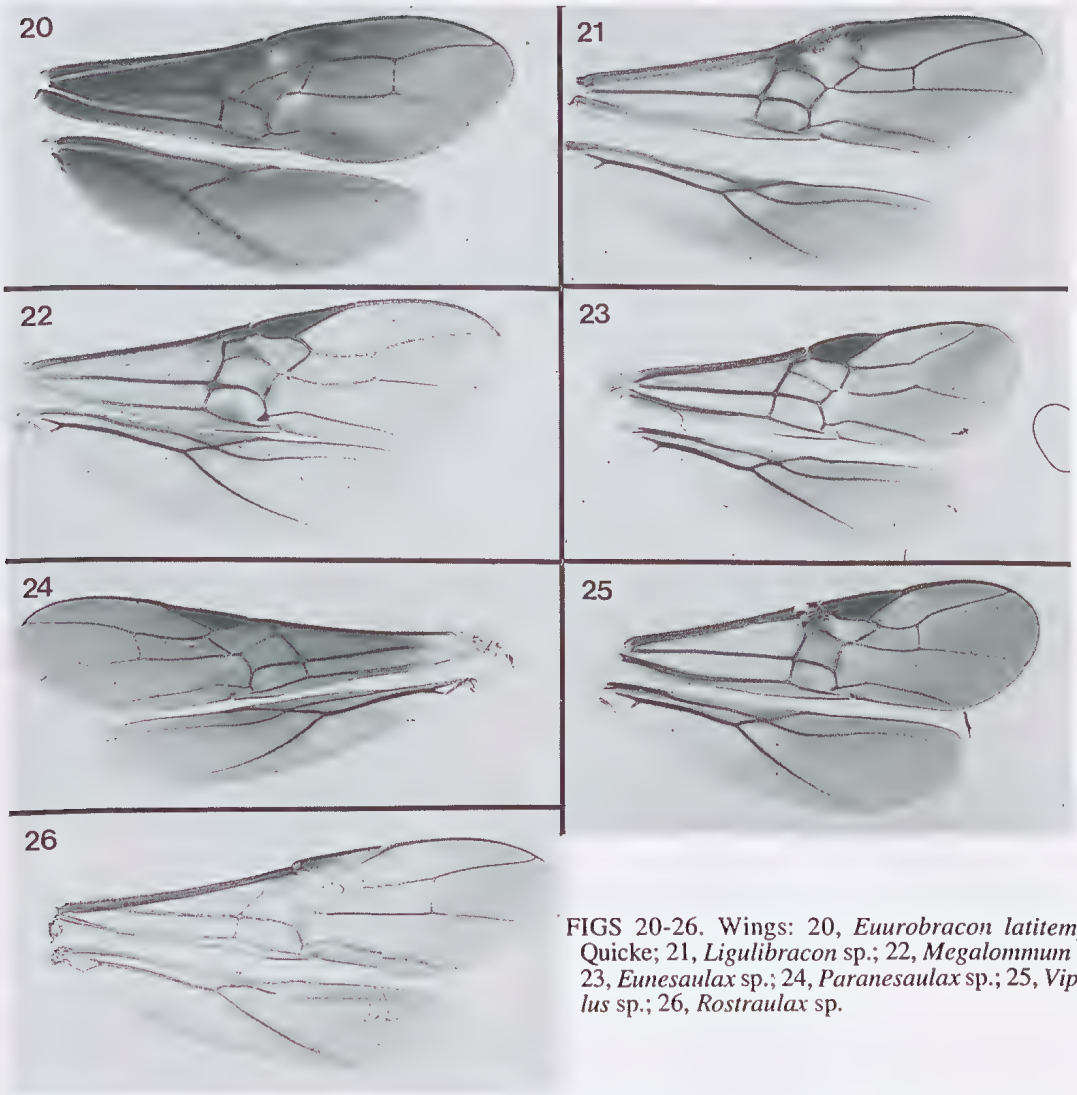
Forewing. Lengths of veins SR1:3-SR:r = 3.5:2.2:1.0. Lengths of veins 2-SR:3-SR:r-m = 1.37:2.2:1.0. Vein r-m with 2 distinct bulli. Vein cu-a antefurcal, strongly bent.

Hindwing. Lengths of veins 1r-m : SC+R1 = 1.05:1.0. Apex of vein C+SC+R with one especially thickened bristle. Vein 2-CU almost reaching wing margin.

Lengths of fore femur: tibia: tarsus = 1.0:1.13:1.33. Lengths of hind femur: tibia: basitarsus = 2.3:2.8:1.0. Hind basitarsus 3.3 times longer than deep.

First metasomal tergite approximately 2.0 times longer than maximally wide, flattened lateral areas of tergum virtually absent sub-posteriorly. Ovipositor (part exserted beyond apex of metasoma) 1.5 times longer than hind basitarsus; 0.1 times length of forewing.

Black except the following which are bright orange-red: pronotum (largely), mesoscutum, scutellum mesopleuron, mesosternum, tegulae, metanotum, posterior of propodeum, apex of fore femur, fore tibia (except spur), fore tarsus, lateral areas of 1st metasomal tergite and 2nd metasomal tergite. Forewing yellow basally, brown apically with yellow pterostigma (Fig. 11).



FIGS 20-26. Wings: 20, *Euurobracon latitempus* Quicke; 21, *Ligulibracon* sp.; 22, *Megalommum* sp.; 23, *Eunesaulax* sp.; 24, *Paranesaulax* sp.; 25, *Vipiellus* sp.; 26, *Rostraulax* sp.

ETYMOLOGY

Named after Richard Willan for his kindness and help during DLJQ's visit to Australia.

Callibracon Ashmead
(Figs 50, 64)

Synonyms. Poecilobacon Cameron syn.nov.

This is a vast, mostly Australian genus of medium-sized to large (and often common) braconines that are greatly in need of taxonomic revision. Previously species were often referred to under the genus *Ipobracon* Thomson (a junior synonym of *Cyanopterus* Haliday). Species have been reared from a variety of wood-boring, coleopterous hosts including Elateridae and Scolytidae, and three species have been collected in association with *Eucalyptus* infested with the cerambycid genus, *Phoracantha* (Quicke, 1989c; Quicke et al., 1992). Some species are gregarious parasitoids.

The genus *Poecilobracon* Cameron (type species: *Poecilobracon flaviceps* Cameron 1901: 122) is treated here as a new subjective synonym of *Callibracon* since examination of a large number of specimens has shown that the characters used by Quicke (1987b) to distinguish between these, viz. scapus length and metasomal sculpture, show great variation and cannot therefore be used as generic characters.

Campyloneurus Szépligeti
(Fig. 62)

Synonyms. Monolcia Enderlein; *Diolcia* Enderlein.

A medium-sized genus of small to medium-sized wasps which are found from India and Japan to Australia. Several species are reported from Australia (Parrott, 1953) but only two appear to be common. Several Australian species included under *Campyloneurus* in the past are referable to *Pycnobraconoides* gen.nov. Australian species of *Campyloneurus* species appear to be largely or perhaps exclusively parasitoids of cerambycid larvae, one Australian species having frequently been reared from members of the cerambycid beetle genus *Zygrita* on a variety of legumes including soya-bean. However, there is a record from grass tree (*Xanthorrhoea*) stems that were infested with both Curculionidae and Cerambycidae. Two host records from India suggest that elsewhere *Campyloneurus* spp. may also attack stem-boring pyralid moth larvae (Quicke, 1989c). The available evidence suggests that at least some species are gregarious parasitoids.

Cedilla Quicke
(Figs 94, 124)

Known from only a single Australian species of medium-sized Aphrastobraconini (Quicke & Tobias, 1990). Nothing is known of its biology though the type specimen of the type species was collected at light indicating that they may be crepuscular or nocturnal as appears to be commonly the case with Australian Aphrastobraconini (Quicke, 1992).

Chaoilta Cameron
(Figs 34, 35, 36, 37, 38, 39, 40, 44, 69)

Synonyms. Blastomorpha Szépligeti; *Platybracon* Szépligeti; *Iphioilta* Ramakrishna Ayyar.

A rather small genus of medium-sized to large braconines. Distributed from India to Australia, most species have been described from Indonesia and New Guinea. The five Australian species were treated by Quicke (1991a); *C.* (*Blastomorpha*) *decorata* Szépligeti is restricted to north Queensland the other four species belonging to the nominal subgenus are more widespread. Nothing is known of the biology of *Chaoilta*. However, the closely related genera *Atanycolus* Foerster, principally from the Holarctic, and *Odontoscapus* Kriechbaumer from the Afrotropical Region are both parasitoids of bark-boring coleopterous larvae, particularly of the families Bostrychidae and Buprestidae (Quicke, 1988b, 1989c).

Curriea Ashmead

A small genus of the tribe Aphrastobraconini originally described from the Afrotropical Region but widespread through the Old World tropics and recorded from Australia for the first time by Quicke (1992). We have seen several Australian species, all of which appear to be undescribed.

Esengoides Quicke

A small genus of the tribe Braconini known from only two species: *E. fulvus* Quicke from Australia (north Queensland) and *E. crenulatus* Quicke from the Solomon Islands (Quicke, 1989b). Small wasps with wing lengths less than 5mm. Nothing is known of their biology.

Eucurriea Quicke
(Figs 28, 31, 43)

A small genus of medium-sized wasps previously confused with *Megalommum* and *Curriea* Ashmead (see Quicke & Tobias, 1990). Frequently collected at light (Quicke, 1992); nothing else is known of their biology.

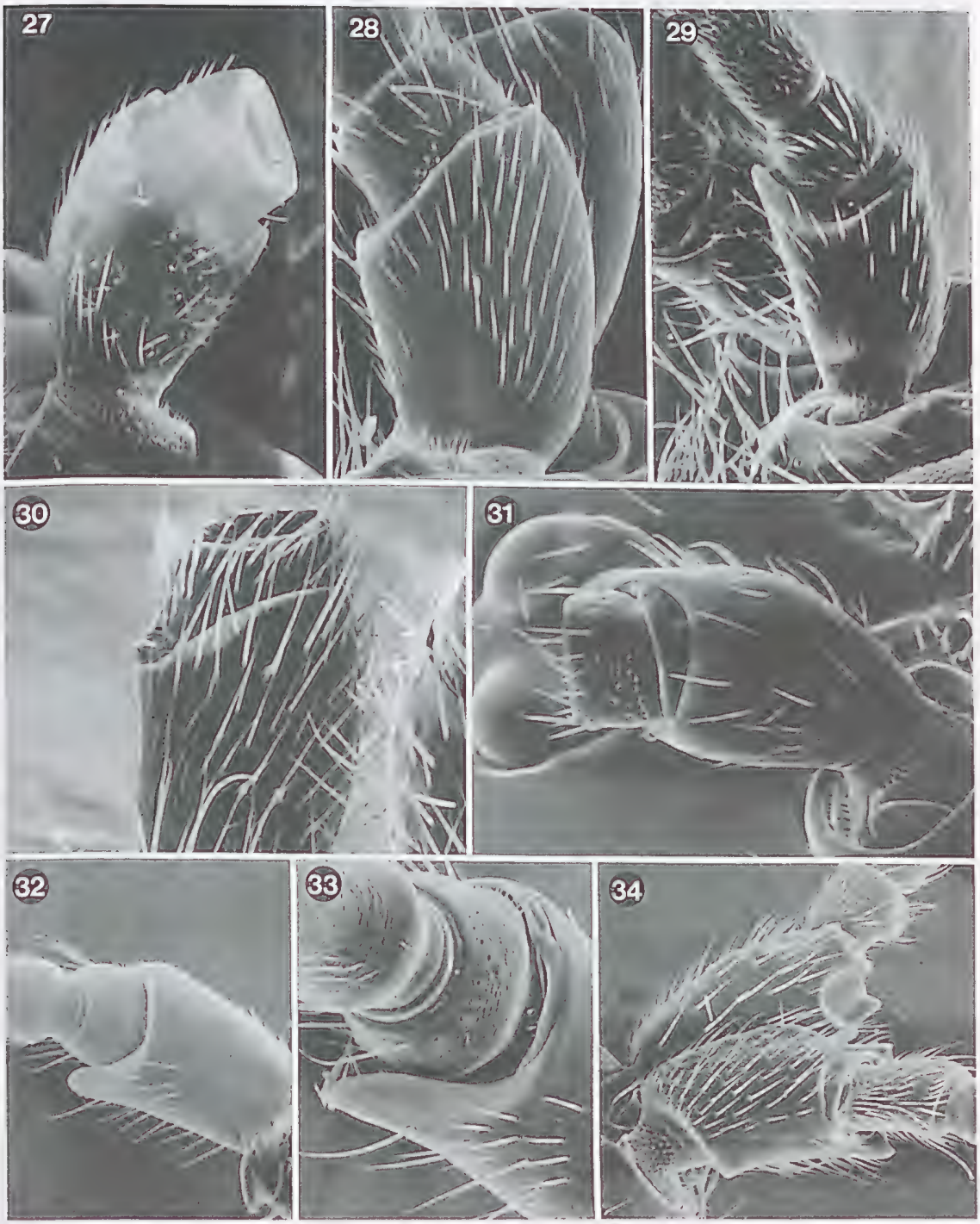
Eunesaulax Tobias
(Figs 7, 23, 60, 68, 135, 136)

A small genus of medium-sized rather slender wasps, known from three Australian species, *E. terebratus* Tobias, *E. nigriventris* Tobias and *E. radialis* Tobias (Quicke & Tobias, 1990). The wing venation is fairly distinctive but the form of the ovipositor apex shows considerable variation (Fig. 135 cf. 136). Nothing is known of their biology and their relationships are still uncertain.

Euurobracon Ashmead
(Figs 20, 48, 56, 96)

Synonyms. Delmira Cameron; *Exobracon* Szépligeti; *Lissobracon* Cameron.

It is not known for certain whether this genus occurs in Australia. A single specimen of *E. latitempus* Quicke was found in a Queensland collection but it lacked data (Quicke, 1989a). However, as *Euurobracon* occurs in Papua New Guinea it is quite likely that it also occurs at least



FIGS 27-34. Features of scapus and pedicellus: 27, *Calcaribracon* sp., medial aspect; 28, *Eucurriea* sp., lateral aspect; 29, *Ligulibracon* sp., lateral aspect; 30, *Hybogaster* sp., ventro-medial aspect; 31, *Eucurriea* sp., medial aspect; 32, *Iphiaulax* sp., lateral aspect; 33, *Iphiaulax* sp., apico-ventro-medial aspect; 34, *Chaoilta (Chaoilta)* sp., lateral and medial aspects.

in far north Queensland. *Euurobracon* species are large wasps, sometimes with extremely long ovipositors (van Achterberg, 1986; Quicke, 1987b), and they have been reared from cerambycid beetle larvae living deep within wood (Quicke, 1989c).

Euurobraconoides Quicke
(Fig. 8)

Medium-sized braconines belonging to the tribe Euurobraconini with wing-lengths between 9 and 11mm. Known from a single Australian (north Queensland) species, *E. longicaudis* Quicke (Fig. 8). Nothing is known of its biology (Quicke, 1988c) but one specimen is labelled as having been collected in rainforest.

*Furcadesha Quicke

Small wasps belonging to the Adeshini. Known only from the type species *F. huddlestoni* from India and *F. walteri* sp.nov. from south-west Queensland. Nothing is known of the biology of any of the Adeshini though both *F. walteri* and the new *Africadesha* (q.v.) species described above were collected by vacuum suction from grass and low herbs.

Key to species of *Furcadesha*

1. Forewing vein SR1 more than 2.4 times longer than vein 3-SR; lateral lobes of mesoscutum extensively setose; mesosoma and metasomal tergites extensively marked with black .... *F. huddlestoni* Quicke
- Forewing vein SR1 less than 1.8 times longer than vein 3-SR; lateral lobes of mesoscutum largely glabrous except postero- medially and along line of notaulus; mesosoma and metasoma entirely brownish yellow to brownish orange .... *F. walteri* sp.nov.

Furcadesha walteri sp.nov.

(Figs 81, 89, 110, 111)

MATERIAL EXAMINED

HOLOTYPE: ♀ with the following labels: 'MT. Nebo, S.E. Queensland. 1.IV. 1974 I.D. Galloway' and 'CAUGHT USING D- VAC SUCTION NET'. Deposited in QMBA (originally from QDPI).

DESCRIPTION (♀)

Length of body 3.1mm, of forewing 3.1mm and of ovipositor (part exserted beyond apex of metasoma) 0.3mm.

First flagellomere 1.25 times longer than the 2nd. Scapus normal, not expanded dorsally. Height of clypeus: inter-tentorial distance: tentorio-ocular distance = 1.0:1.6:1.35. Height of eye: width of face: width of head = 1.0:1.35:2.5. Face smooth. Horizontal length of eye: horizontal length of head behind eye = 2.8:1.0. Head strongly narrowed behind eye. Shortest distance between posterior ocelli: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.6:1.0:3.3.

Mesosoma 1.65 times longer than high. Mesoscutum setose medio- posteriorly and along lines of notauli. Notauli deeply impressed, minutely crenulate. Medio-posterior part of mesoscutum rugose, otherwise mesoscutum smooth and shiny. Precoxal suture virtually absent, mesopleuron and mesosternum largely smooth and shiny.

Forewing. Lengths of veins SR1:3-SR:r = 7.25:4.5:1.0. Lengths of veins 2-SR:3-SR:r-m = 1.1:2.0:1.0. Vein 2-SR+M short; shortest distance between 1st subdiscal cell and 2nd submarginal cell: length of vein m-cu = 1.0:2.7. Vein cu-a interstitial. Vein 3-CU1 slightly postfurcal with respect to m-cu.

Base of hindwing evenly setose. Posterior margin of hindwing distinctly emarginate.

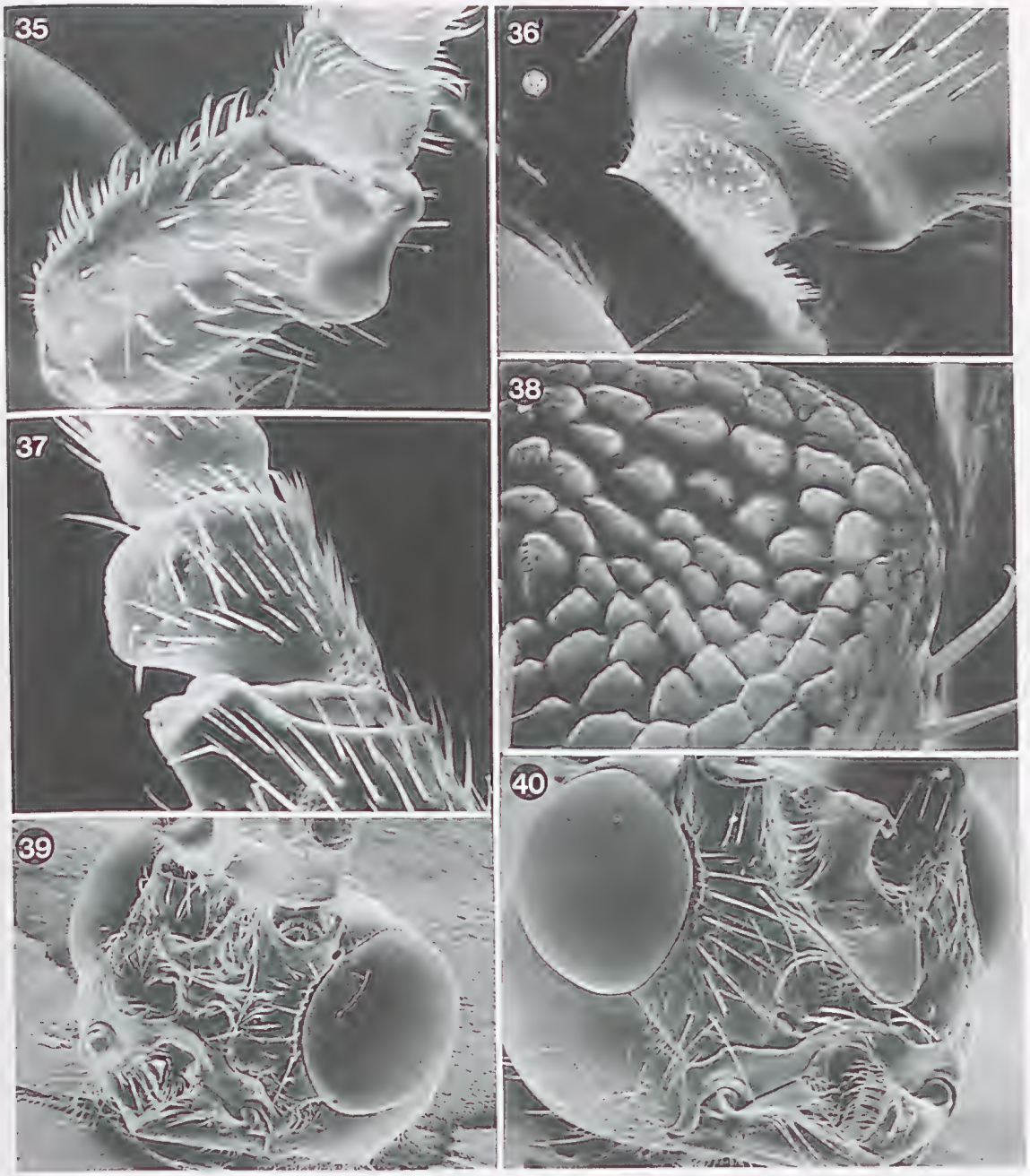
Lengths of fore femur: tibia : tarsus = 1.0:1.29:1.52. Lengths of hind femur: tibia: basitarsus = 1.3:2.4:1.0. Hind basitarsus 9 times longer than maximally deep.

Metasomal tergites largely evenly sculptured with fine, anastomosing, longitudinal ridges separated by rows of punctures (as in *huddlestoni* Quicke), but 5th tergite with longitudinal striation weaker and less regular. First tergite 1.1 times longer than posteriorly wide. Second tergite 1.5 times wider posteriorly than medially long. Posterior margin of 5th tergite with well-developed perimedial projections and with lateral emarginations.

Yellowish-brown except for antennae and apices of tarsi which are piceous and ovipositor sheaths which are black. Wings slightly hyaline with brown venation.

ETYMOLOGY

Named in honour of the senior author's father, Walter Jesse Quicke, for his years of patience.



FIGS 35-40. Features of scapus, pedicellus and face: 35, *Chaoilta (Chaoilta)* sp., scapus and pedicellus apico-medial aspect; 36, *Chaoilta (Chaoilta)* sp., base of scapus, lateral aspect; 37, *Chaoilta (Chaoilta)* sp., pedicellus, medial aspect; 38, *Chaoilta (Blastomorpha) decorata*, detail of apical part of pedicellus; 39, *Chaoilta (Chaoilta)* sp., head; 40, *Chaoilta (Blastomorpha) decorata*, head.

*Gelasinibracon Quicke
(Figs 45, 71, 73, 10)

Small braconines of the tribe Braconini with wing lengths less than 6mm. Known only from two closely related species: *G. sedlaceki* Quicke from Papua New Guinea and north Queensland and *G. simplicicaudatus* Quicke, only known

from Papua New Guinea (Quicke, 1989b). Nothing is known of their biology.

Habrobracon Ashmead
(Fig. 86)

Habrobracon is closely related to *Bracon*, which is probably paraphyletic because *Habrobracon* is classified separately. Cosmopolitan group of small wasps, with about twenty described species. Several species have been employed as biological control agents principally against stored product pests and *H. gelechiae* (Ashmead) has been introduced into Australia. *H. hebetor* (Say) is also recorded from Australia where it has been reared from *Cactoblastis cactorum.*

Hybogaster Szépligeti
(Figs 18, 30, 47, 67, 128)

Large wasps apparently related to the Euurobraconini (Quicke, 1988a). A principally Indo-Australian genus but with one species occurring in South Africa (Quicke, 1988a) and another in north Queensland. It should be noted however, that Parrott's (1953) record of *Hybogaster* from Australia is a misidentification of *Iphiaulax australiensis* Ashmead (Quicke, 1991a). Nothing is known of the biology of *Hybogaster* species but members of the related genus *Zeuzerilia* van Achterberg are parasites of Cossidae (van Achterberg, 1989).

Hyboteles van Achterberg
(Figs 72, 74, 105, 115)

Small wasps belonging to the subtribe Aspidobraconina of the Braconini. *Hyboteles* ranges from Brunei and the Philippines to north Australia and is monophyletic. Probably all Aspidobraconina are endoparasitoids of butterfly pupae; *Hyboteles toxopeusi* van Achterberg has been reared as a solitary endoparasitoid from a lycaenid pupa in Papua New Guinea (Quicke, 1987a, 1988b).

Iphiaulax Foerster
(Figs 32, 33, 63, 129)

Synonyms. Aniphiaulax Kokoujev; *Iphiaulacidea* Fahringer; *Euglyptobracon* Telenga

A large and virtually cosmopolitan genus of medium-sized braconines. Eight Australian species were treated by Quicke (1991a); several of these had previously been wrongly placed in *Cyanopterus* Haliday or *Hybogaster* Szépligeti. Subsequently, the senior author has seen specimens of two undescribed Australian species in the collection of the AEIG. Nearly all members of the genus appear to be specialized parasitoids of cerambycid beetle larvae (Quicke, 1988b) but van Achterberg (1989) reported one species as having been reared from cossid moth larvae. Some species are frequently collected amongst mangroves and females are capable of giving a painful sting (DLJQ, pers. obs.).

Ligulibracon Quicke
(Figs 21, 42, 55, 88, 123)

A small genus of medium-sized to large Aphrastobraconini entirely restricted to Australia; apparently only the type-species, *L. levor* Quicke, is described though several others have been seen in collections by the senior author. Nothing is known of the biology of *Ligulibracon*, though, in common with other Australian Aphrastobraconina, they seem to be at least partially nocturnal (Quicke, 1992).

Macrobracon Szépligeti
(Figs 57, 58)

A small genus of large braconines belonging to the *Mesobracon* Szépligeti group (see Quicke, 1987b). *Macrobracon* ranges from north Queensland to south India; only one species, *M. nobilis* Turner, occurs in Australia (Shenefelt, 1978). Nothing is known of the biology of *Macrobracon* though members of the related oriental genus *Pseudoshirakia* van Achterberg attack stem-boring pyralid moth larvae in grain crops (Achterberg, 1983).

Megalommum Szépligeti
(Figs 22, 41, 49, 61)

Medium-sized species of Aphrastobaconini primarily from Australia, where there are many undescribed species, but also occurring in Papua New Guinea. Frequently collected at light (Quicke, 1992). The ovipositors of members of this genus collectively display a great deal of variation in length and shape but typically lack apico-ventral serrations probably indicating that oviposition takes place into a soft substrate.

Mollibracon Quicke
(Figs 17, 133)

A monotypic genus of medium-sized wasps entirely restricted to Australia. *M. bimaris* (Turner) has been reared as a parasitoid of curculionid larvae, *Meriphus longirostris*, in *Banksia* cones (Quicke, 1988b). Most specimens seen by us are from Western Australia.

Myosoma Brullé
(Figs 2, 54, 70)

Synonyms. Acanthobracon Kriechbaumer; *Amyosoma* Viereck

A largely neotropical genus of small to medium-sized Braconini but with a few mostly smaller species known from the Old World tropics (Quicke & Wharton, 1989). *Myosoma rufescens* is the first true record of this genus in Australia (see Quicke, 1988b); *M. mutator* (Fabricius) belongs to *Pycnobraconoides* gen.nov. *Myosoma* spp. appear to be principally parasitoids of concealed pyralid moth larvae (Shenefelt, 1978; Quicke & Wharton, 1989) but *M. chinensis* has also been reared from the larvae of the cossid *Zeuzera* in India, and *M. yanoi* (Watanabe) has been reared from larvae of the sesiid *Paranthrene regale* in Japan (Maetô, 1992).

Key to Indo-Australian species of *Myosoma*

1. Metasomal tergites 1-5 bright orange contrasting strongly with piceous or black tergites 6-9 (Fig. 2); head largely black .....*M. rufescens* sp.nov.
- Metasomal tergites unicolorous piceous or black; head variably coloured .....
.....*M. chinensis* (Szépligeti) & other spp.

Myosoma rufescens sp.nov.
(Fig. 2)

MATERIAL EXAMINED

HOLOTYPE: ♀ with the following labels: 'AUSTRALIA: ACT Canberra, Black Mtn. Jan 25-30. 1984 L. Masner, MT' & 'Dry sclerophyl Eucalyptus for.' From AEIG but on permanent loan to ANIC by agreement with collections manager.

PARATYPE: ♂ with following labels: 'QUEENSLAND: Mirani 34km NW Mackay X-16-79' and 'HE & MA Evans & A. Hook Coll.'. ANIC.

DESCRIPTION (♀)

Length of body 5.7mm, of fore wing 5.5mm and of ovipositor (part exserted beyond apex of metasoma) 1.3mm.

First flagellomere 1.07 times longer than both the 2nd and 3rd separately. Third flagellomere 1.4 times longer than wide. Height of clypeus: intertentorial distance: tentorio-ocular distance = 1.0: 3.7: 2.3. Face smooth medially; coriaceous and densely setose laterally. Height of eye: shortest distance between eyes: width of head = 1.05:1.0:2.0. Frons densely setose except along the median line. Post-ocellar line: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.4:1.0:3.57. Occiput largely glabrous. Horizontal length of eye 1.7 times horizontal length of head behind eye.

Mesosoma 1.5 times longer than high. Notauli weak but impressed along whole length of mesoscutum. Lateral lobes of mesoscutum glabrous.

Forewing. Lengths of veins SR1:3-SR: r = 3.9: 3.0: 1.0. Lengths of veins 2-SR:3-SR:r-m = 1.1: 2.0: 1.0. Pterostigma 3.15 times longer than maximally wide. Vein cu-a virtually interstitial. Vein 1-SR+M straight.

Hindwing. Lengths of veins 1r-m: SC+R1 = 1.0:1.7. Apex of vein C+SC+R with one especially thickened bristle. Base of wing evenly setose.

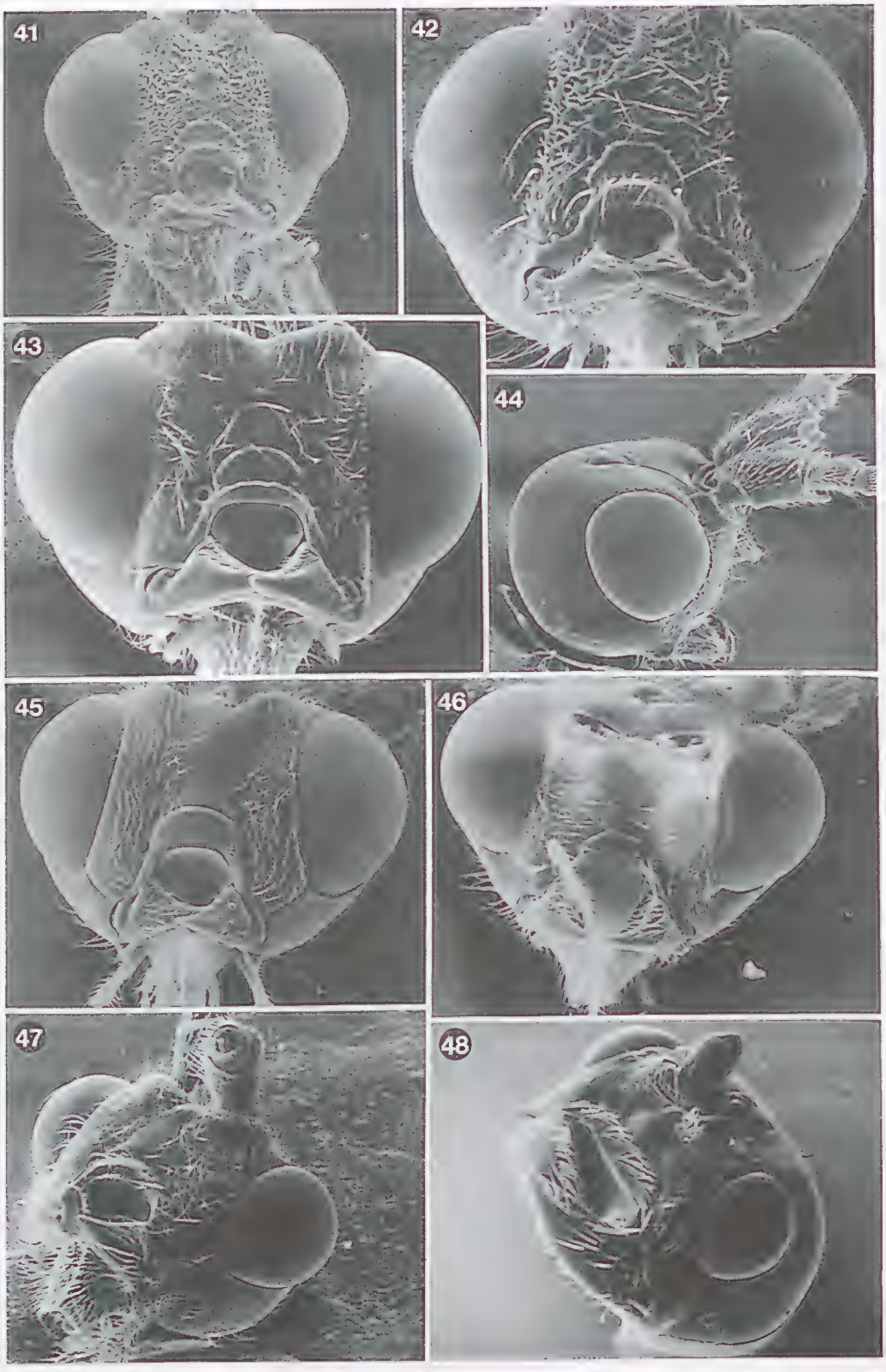
Lengths of fore femur: tibia: tarsus = 1.0: 1.1: 1.3. Lengths of hind femur:tibia:basitarsus = 1.9: 2.8 :1.0. Hind femur 3.2 times longer than maximally wide. Hind tarsus 7.0 times longer than maximally wide. Hind basitarsus 6.5 times longer than apically deep.

Metasoma smooth and shiny. First tergite approximately 2.2 times longer than maximally wide; lateral areas narrow but complete. Second tergite with antero-lateral corners with reduced sclerotization. Second suture straight, narrow, quite deep. Tergites 3 to 6 with irregular, sparse, short setosity posteriorly.

Pale orange brown to brownish yellow except for the following which are black or piceous: antennae; head except labio-maxillary complex, palps and base of mandibles; mid- and posterior legs; metasomal tergites 6 and 7; ovipositor sheaths. Wing membrane pale brown slightly paler distally; venation and pterostigma dark brown.

DESCRIPTION (♂)

As for female except slightly smaller and the middle leg is brownish yellow except for the telotarsus which is piceous.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*Paranesaulax Quicke
(Figs 24, 99, 106, 127)

Medium-sized braconines known from only one described species from Papua New Guinea, *P. nitor* Quicke. A possibly conspecific individual from north Queensland has been seen by the authors. Nothing is known of the biology of this genus.

Pedinopleura van Achterberg
(Figs 78, 114, 121, 122)

Small species belonging to the Aspidobraconina. In addition to *P. australiensis* sp.nov., two non-Australian species have been described (Achterberg, 1984) but many undescribed ones occur in South Africa, India through Malaysia to New Guinea and north Australia. There are no host records for this genus but three other genera of the Aspidobraconina (*Aspidobracon* van Achterberg, *Hyboteles* van Achterberg and *Philomacroploea* Cameron) have been reared from butterfly pupae (van Achterberg, 1984; Quicke, 1987a).

Key to the Indo-Australian species of *Pedinopleura* (♀♀ only)

1. Face, frons, temples and vertex smooth; lateral margin of syntergite 1+2+3 with an obvious notch (Fig. 122); antenna largely brownish becoming piceous apically ...*P. emarginata* van Achterberg
   - Face, frons, temples and vertex striate (Fig. 78); lateral margin of syntergite 1+2+3 without notch, evenly curved or with a single posterior lobe (Fig. 121); antenna black 2
2. Metasomal tergites 3-5 with a dark spot on either side; posterior margin of 6th metasomal tergite with a well-developed emargination; lateral margin of syntergite without a posterior lobe; frons and vertex coarsely transversely striate ....*P. koshuensis* (Watanabe)
   - Metasomal tergites 3-5 unicolorous brownish yellow; posterior margin of 6th metasomal tergite only very weakly emarginate (Fig. 114); lateral margin of syntergite with a well-developed posterior lobe (Fig. 121); frons and vertex very finely transversely striate (Fig. 78) ....*P. australiensis* sp.nov.

Pedinopleura australiensis sp.nov.
(Figs 78, 114, 121)

MATERIAL EXAMINED
HOLOTYPE: ♀ with following labels: 'Ayr Queensland 4 Sep. 1950 E.F.Riek'. Deposited in ANIC.
PARATYPE: ♂ with same data as holotype. ANIC.

DESCRIPTION (♀)
Length of body 4.5mm, and of forewing 4.3mm, of ovipositor (part exserted beyond apex of metasoma) 1.1mm and of antenna 4.1mm.

Antenna with 36 flagellomeres. Terminal flagellomere pointed but not acuminate, 2.1 times longer than basally wide. Median flagellomeres approximately as wide as long. First flagellomere 1.3 times longer than both the 2nd and 3rd separately, the latter being 1.2 time longer than wide. Height of clypeus: inter- tentorial distance: tentorio-ocular distance = 1:2:2. Height of eye: width of face: width of head = 1.0:1.5:1.77. Malar suture deep and narrow. Face with multiple, strong, parallel, transverse ridges. Eyes virtually glabrous. Frons and occiput finely subtransversely carinate. Head very transverse; horizontal length of head behind eye: horizontal length of eye = 2.35:1.0 Post- ocellar length: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.0:1.0:2.75.

Mesosoma 1.4 times longer than high; strongly sculptured, mostly punctate. Median area of metanotum with a complete mid- longitudinal carina. Precoxal suture not impressed; indicated by a band of punctures. Propodeum with a complete mid-longitudinal carina bordered by short, rather weak crenulations.

Forewing. Lengths of veins SR1:3-SR:r = 7.3:2.8:1.0. Lengths of veins 2-SR:3-SR:r-m = 1.1:1.7:1.0 Vein 2-SR+M long, shortest distance between 1st discal cell and 2nd submarginal cell: length of vein m-cu = 1.7:1.0. Vein cu-a interstitial.

Length of fore femur: tibia: tarsus = 1.0:1.0:1.15. Length of hind femur: tibia: basitarsus = 1.94: 2.65: 1.0. Hind basitarsus 4.9 times longer than deep.

Metasoma with strong rugose sculpture. First tergite with a distinct median groove posteriorly. Posterior margin of 6th tergite very weakly emarginate. Ovipositor (part exserted beyond apex of metasoma) approximately 0.4 times length of forewing.

FIGS 41-48. Features of head: 41, *Megalommum* sp.; 42, *Ligulibracon* sp.; 43, *Eucurriea* sp.; 44, *Chaoilta (Chaoilta)* sp.; 45, *Gelasinibracon* sp.; 46, *Pycnobraconoides mutator* (Fabricius); 47, *Hybogaster* sp.; 48, *Euurobracon latitempus* Quicke.

Entirely honey-yellow except for antennae, hind tarsi, and ovipositor sheaths which are black or piceous. Wing membrane pale yellow tending to hyaline distally; vein C+SC+R and pterostigma piceous, remainder of venation yellowish.

DESCRIPTION (♂)

Very similar to female except smaller and posterior margin of 6th metasomal tergite only marginally emarginate and antenna dark rufous.

Ploceibracon Quicke
(Figs 75, 79, 100)

Known only from the type species, *P. monstrans* Quicke, from New South Wales. The holotype of *P. monstrans* has a small dark mark indicating a trace of hindwing vein 3-CU and, together with the strong spur from fore-wing vein 3-CU1, this may indicate a relationship with *Calcaribracon.* Nothing is known of its biology.

Psittacibracon Quicke
(Figs 9, 10, 132)

A rare monotypic genus of medium-sized Braconini entirely restricted to Australia. *Psittacibracon lacteolus* Quicke (Figs 9, 10) is known from a few specimens from South Australia, Western Australia and New South Wales. Nothing is known of its biology.

Pycnobraconoides gen.nov.
(Figs 6, 46, 130)

TYPE SPECIES

Ichneumon mutator Fabricius 1775: 335.

DIAGNOSIS

Pycnobraconoides can be distinguished from other members of the tribe Braconini (sensu van Achterberg, 1983) by the following combination of characters: (i) head very transverse; (ii) eyes usually moderately to very setose; (iii) precoxal suture absent; (iv) hindwing vein 1r-m much shorter than vein SC+R1(v) 2nd submarginal cell of forewing long; (vi) claws with rounded basal lobes; (vii) propodeum simple, without a mid-longitudinal carina; (viii) metasoma robust, 3rd tergite more than 2 times wider than long; (ix) ovipositor robust, without a pre-apical dorsal nodus but distinctly pre-apically expanded (Fig. 130); (x) mandibles (except for apex) white.

GENERIC DESCRIPTION

Antennae shorter than forewing, with approximately 40 flagellomeres. Terminal flagellomere acuminate. Median flagellomeres marginally longer than wide. Scapus small, shorter ventrally than dorsally in lateral aspect; not apico-medially emarginate. Labio-maxillary complex short. Mandibles ivory-white except for darker apex. Clypeus angled into hypoclypeus but without a transverse median carina: separated from face dorsally by a groove. Face smooth and shiny, setose. Eyes usually moderately to very densely setose; distinctly emarginate. Frons weakly impressed, largely setose, with a well-developed mid- longitudinal sulcus. Head very transverse; horizontal length of eye approximately 2.5 times longer than horizontal length of head behind eye.

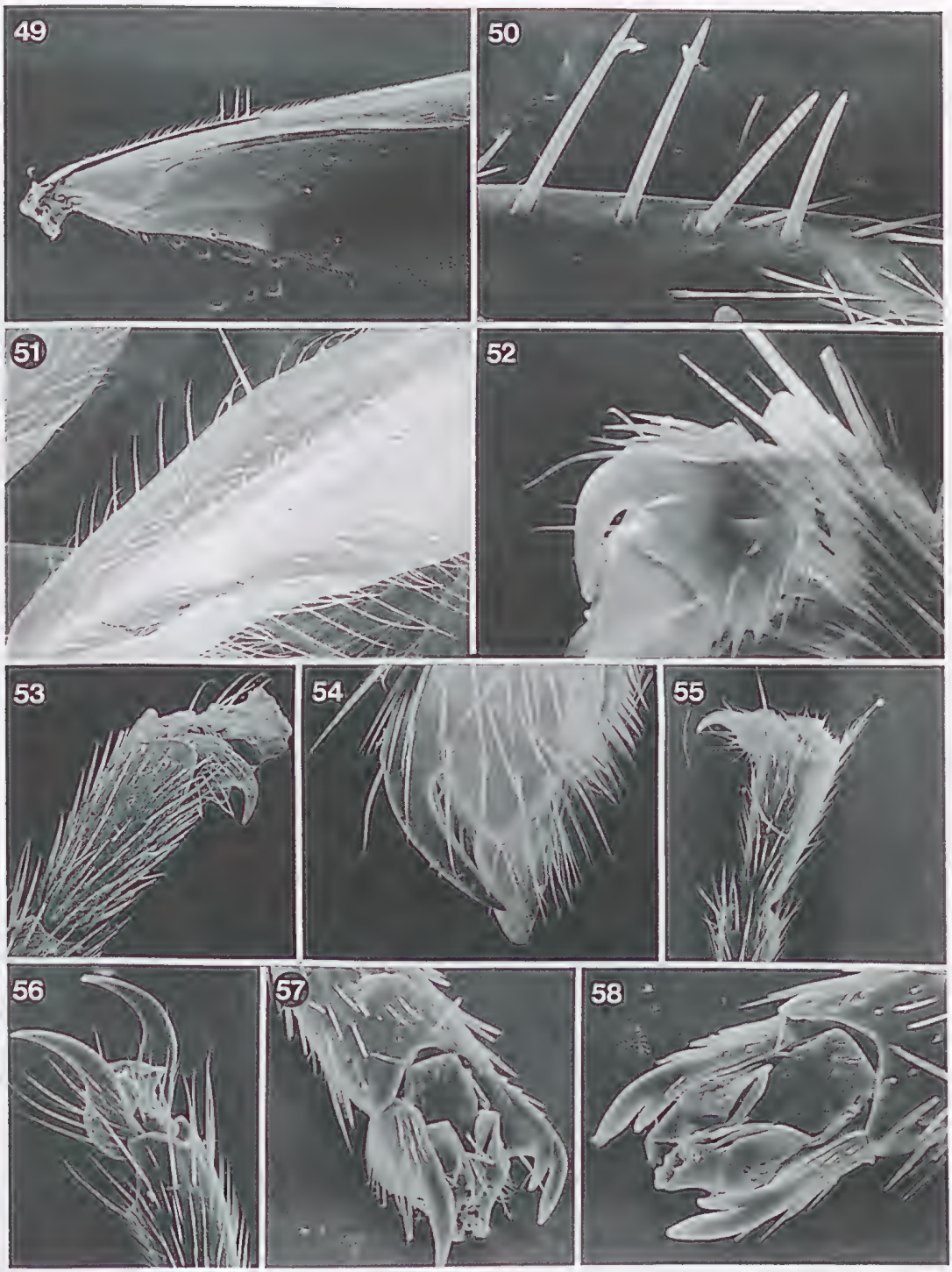
Mesosoma smooth and shiny approximately 1.3 times longer than high. Mesosotum largely glabrous except for along line of notauli. Notauli weakly impressed anteriorly, not impressed posteriorly. Scutellar sulcus narrow, crenulate. Precoxal suture absent. Mesopleural suture smooth. Median area of metanotum not carinate. Propodeum without carinae. Propodeal spiracle small, round, situated near middle of propodeum.

Forewing. Vein 1-SR+M more or less straight. Vein 2-SR+M short, more or less interstitial. Second submarginal cell long, vein 3- SR approximately 0.8 times length of vein SR1. Veins C+SC+R and 1-SR forming an angle of approximately 75°. Vein r- m unsclerotized. Vein cu-a interstitial.

Hindwing. Vein 1r-m much shorter than vein SC+R1. Apex of vein C+SC+R with only one especially thickened bristle. Base of wing evenly setose.

Claws with rounded basal lobes. Hind tibia slender, with indistinct longitudinal, lateral groove.

Metasoma short, wide, robust, largely with rugose to strong punctate sculpture but largely smooth in some species. First tergite with dorsolateral carinae; raised median area sculptured posteriorly, strongly sloping, smooth anteriorly. Second tergite wide, with or without elongate median area (defined largely by difference in sculpture); anterolaterally with a pair of longitudinal, sub-parallel grooves. Tergites 3 to 5 with posterior margins rounded in profile, rarely 5th with a weak transverse, subposterior groove. Ovipositor robust, pre-apically smoothly expanded pre-apically (Fig. 130), ventral valves without or with extremely reduced serrations; part exserted



FIGS 49-58. 49-51, apex of hindwing vein C+SC+R showing specialised bristles: 49, *Megalommum.*; 50, *Callibracon* sp.; 51, *Bracon* sp. 52-58, features of claws: 52, *Calcaribracon willani* sp.nov.; 53, *Bracon* sp.; 54, *Mysosoma* sp.; 55, *Ligulibracon* sp.; 56, *Euurobracon* sp.; 57-58, *Macrobracon* sp.

beyond apex of metasoma slightly shorter than medial length of metasomal tergite 2+3.

MALES

Very similar to females. Intertergal metasomal glands well-developed with a pair of large sac-like reservoirs (Quicke, 1990). Genitalia: digitus with a single apical tooth; parameres with only a single row of setae apically.

BIOLOGY

From many, largely unpublished, records it is clear that *Pycnobraconoides* gen.nov. is a specialised parasitoid of cryptocephaline chrysomelid beetle larvae (Quicke, 1988b). The beetle larvae (and pupae) live in a case from which single specimens of *Pycnobraconoides* commonly emerge. The following cryptocephalines have been recorded as hosts of various species of *Pycnobraconoides*:'*Cadmus*' *aurantiacus*, *Cryptocephalus speciosus*, *Lachnabothra* sp., and *Prasonotus* sp. It is presumed but not proven that *Pycnobraconoides* is ectoparasitic.

DISCUSSION

Pycnobraconoides gen.nov. appears to be most closely related to the oriental genus *Pycnobracon* Cameron which was originally described from India (Cameron, 1902), and recently members of the new genus have been dealt with under *Pycnobracon*. However, it has been recognised for some time that the Australian representatives do not fit well in *Pycnobracon*. Indeed, Quicke (1987b) considered *Pycnobracon* to comprise two sections: those keying out at couplet 108 (loc. cit.), which are referable to *Pycnobracon* sensu stricto; and those keying out at couplets 90 and 94, which are placed here under *Pycnobraconoides* gen.nov. In particular, *Pycnobraconoides* differs from *Pycnobracon* in having a robust ovipositor without a pre-apical dorsal nodus and an extremely transverse head. The biologies of the two genera also differ considerably with *Pycnobracon* sensu stricto parasitic on pyralid moth larvae while *Pycnobraconoides* attacks case-bearing Chrysomelidae (see above). Within Australia, the new genus is widely distributed and specimens representing a small number of species have been seen from Australian Capital Territory, Queensland, New South Wales, Tasmania and Western Australia.

INCLUDED SPECIES

Pycnobraconoides froggattii (Cameron) comb.nov. (= *Bracon froggattii* Cameron, 1911: 339); holotype in BMNH examined.

Pycnobraconoides mutator (Fabricius) comb. nov. (= *Iphiaulax bipartitus* Szépligeti 1905:35; junior subjective synonym, Quicke, 1991c).

*Rostraulax Quicke
(Fig. 104)

Rostraulax species are medium-sized wasps found primarily in Indonesia and New Guinea. One species, *R. xanthocephalus* (Turner), is found in Queensland and northern New South Wales rainforests as well as in Papua New Guinea. Nothing is known of the biology of *Rostraulax* but the apparently related genus *Cratobracon* has been reared from wood-boring cerambycid larvae (Quicke, unpubl. obs.). *Rostraulax* is very closely related to *Shelfordia* Cameron and may need to be synonymized with that genus (van Achterberg, pers. comm.).

Serratobracon Tobias
(Figs 83, 85, 107)

This genus is known from only a single specimen from the Northern Territory which has a highly characteristic combination of pedicellus and scapus morphology. Its affinities were discussed by Tobias in Quicke & Tobias (1990), who concluded that it may be related to either *Sylvibracon* Quicke or to the *Atanycolus* group of genera (Quicke, 1987b). However, neither of these placements is satisfactory and more material needs to be studied.

Simplicibracon Quicke
(Figs 5, 76, 102)

Previously, species of this genus were only known from Taiwan (Quicke, 1988e) and Japan (Maetô, 1991). In addition to these and the new Australian species, the senior author has seen specimens of another new species from Fiji. In *Simplicibracon*, the strongly developed transverse median clypeal carina (Fig. 76) is quite distinctive and most species (except for two seen from Japan) have hind wing vein 2-SC+R slightly transverse. The one species for which the biology is known, *S. curticaudis* Maetô, is a parasitoid of leaf-galling Cecidomyiidae on broad- leaved, evergreen trees (Maetô, 1991).

Key to the species of *Simplicibracon* (♀♀ only)

1. Hindwing vein 2-SC+R longitudinal (see Fig. 101); ovipositor (part exserted beyond apex of metasoma) less than 0.25 times length of forewing; metasomal tergites unicolorous brownish yellow to yellowish brown; 2nd metasomal tergite less than 1.8 times wider than medially long ....*S. curticaudis* Maetô
   - Hindwing vein 2-SC+R transverse (Fig. 102); ovipositor (part exserted beyond apex of metasoma) more than 0.35 times length of forewing; metasomal tergites brownish yellow to whitish yellow, marked with brown or black blotches on tergites 2 and 3 or 3 and 4; 2nd metasomal tergite more than 1.8 times wider than medially long 2
2. Notauli crenulate; metasomal tergites metasomal tergites 5-7 yellow-brown, same as tergites 1 and 2 .....*S. maculigaster* Quicke
   - Notauli smooth; metasomal tergites 5-7 cream-white, different from tergites 1 and 2 ....*S. nigritarsus* sp.nov.

Simplicibracon nigritarsus sp.nov.
(Figs 5, 76, 102)

MATERIAL EXAMINED

HOLOTYPE: ♀ with the following labels: '15.41S 145.12E Annan Riv. 3Km WbyS Black Mt. 26-27 Apr. 1981Q, I.D. Naumann ex ethanol' & 'collected at light'. Deposited in ANIC.

DESCRIPTION (♀)

Length of body 4.2mm, of fore wing 4.6mm, of ovipositor (part exserted beyond apex of metasoma) 1.9mm, and of antenna 4.1mm.

Antennae with 32 flagellomeres. First flagellomere 1.3 times longer than both the 2nd and 3rd separately, the latter being 1.5 times longer than wide. Transverse median clypeal carina strongly protruding. Height of clypeus (upper part): intertentorial distance: tentorio-ocular distance = 1.0:1.82:1.63. Face shiny with moderately well-developed punctures at the bases of the setae. Height of eye (measured parallel to face): width of face: width of head = 1.0:1.18:2.36. Face 2 times wider than high. Eyes weekly setose. Frons without a mid-longitudinal ridge; weakly impressed. Shortest distance between posterior ocelli: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.43:1.0:3.14.

Mesosoma 1.24 times longer than high. Pronotum largely smooth and shiny with narrow crenulate groove laterally. Mesonotum moderately setose posteriorly and laterally but anterior third of middle lobe virtually glabrous. Notauli moderately impressed, not crenulate. Precoxal suture represented by only a weak rounded depression.

Forewing. Lengths of veins SR1:3-SR:r = 5.6:1.9:1.0. Lengths of veins 2-SR: 3-SR: r-m = 1.6:1.9:1.0. Vein r-m with only a single posterior bulla and associated flexion line. Length of vein m-cu: shortest distance between 1st subdiscal cell and 2nd submarginal cell = 0.8:1.0.

Hindwing. Base of wing more or less evenly, densely setose. Vein 2-SC+R distinctly transverse. Apex of vein C+SC+R with only one especially thickened bristle.

Lengths of fore femur: tibia: tarsus = 1.0:1.13:1.3. Fore tibia moderately densely with strong spine-like setae antero-laterally. Lengths of hind femur: tibia: basitarsus = 1.8:2.55:1.0. Hind tibia very robust, 6.1 times longer than maximally deep. Hind basitarsus 4.4 times longer than deep.

Metasoma with rugulose sculpture. Second tergite 2.1 times wider than medially long. Ovipositor (part exserted beyond apex of metasoma) approximately 0.4 times length of forewing.

Brownish yellow except for the following: antennae, hind tibia except extreme base, hind basitarsus, a pair of large submedial marks on the 3rd and 4th tergites, ovipositor sheaths, black. Lateral parts of 3rd and 4th tergites and all except for a mid- longitudinal yellow line on tergites 5 to 7, white. Wings pale smoky brown with brown venation.

NOTE

The holotype of *S. nigritarsus* sp.nov. is the same specimen as referred to by Quicke (1992).

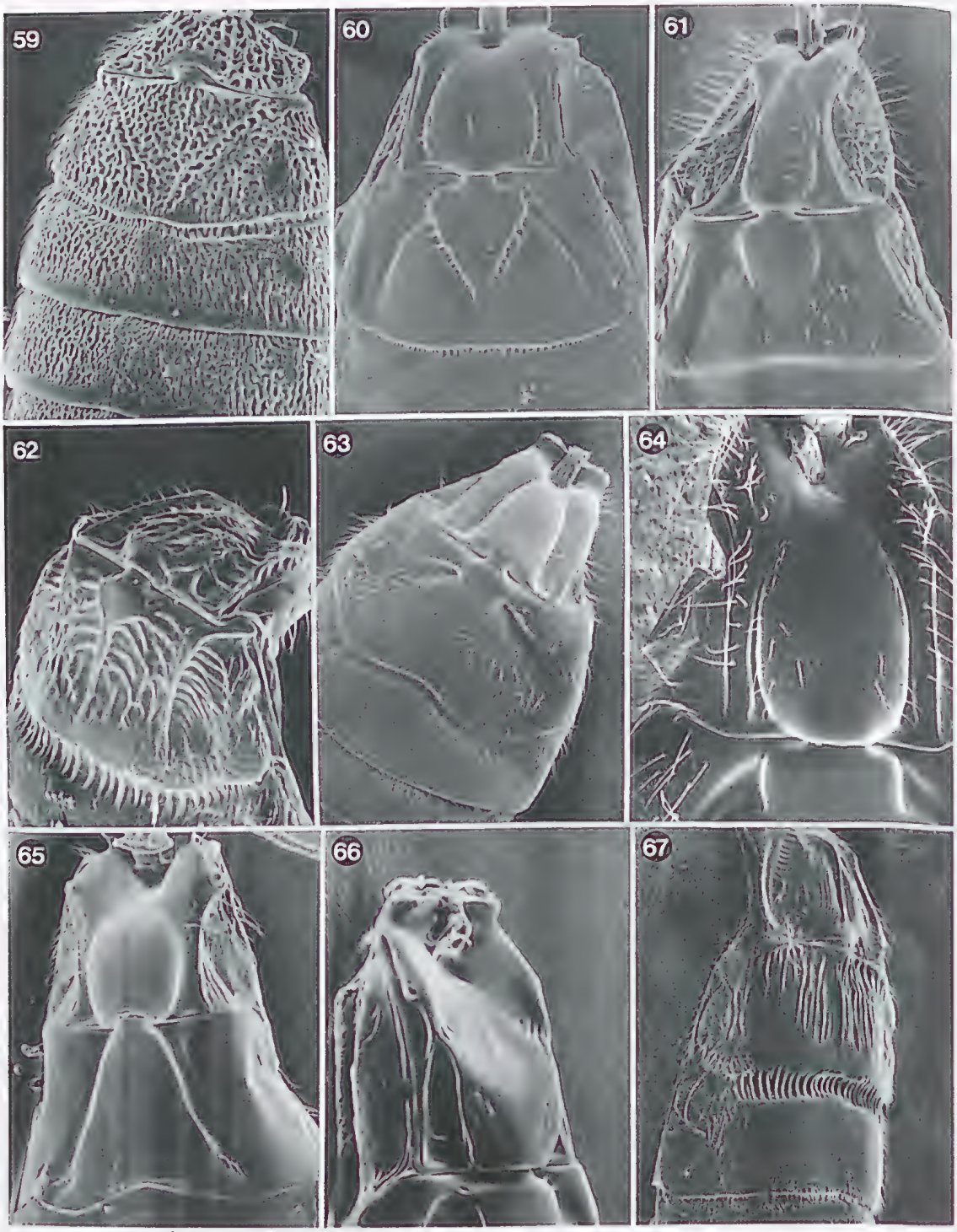
Stenobracon Szépligeti
(Fig. 93)

Synonyms. Elphea Cameron; *Phanaulax* Cameron.

A small genus of medium-sized wasps belonging to the tribe Bathyaulacini. One probably undescribed species is found in the north of Western Australia in the Kimberleys. Elsewhere, *Stenobracon* spp. are important parasitoids of Lepidoptera larvae that bore in stems of grain crops (Quicke, 1983; 1988c) but nothing is known about the biology of the Australian species.

Stigmatobracon Turner
(Figs 1, 131)

A small genus of medium-sized to large wasps.



FIGS 59-67. Features of the metasoma: 59, *Tropobracon* sp. (African) T1-T4; 60, *Eunesaulax* sp., T1-T2; 61, *Megalommum* sp., T1-T2; 62, *Campyloneurus* sp., Tj1- T2; 63, *Iphiaulax* sp., T1-T3; 64, *Callibracon* sp., T1; 65, *Virgulibracon* sp., T1-T2; 66, *Vomeribracon* sp., T1; 67, *Hybogaster* sp., T1-T4.

A key to the four described species, all from Australia, is provided by Turner (1918). However, the senior author has seen a female of *S. xanthostigma* Turner from Papua New Guinea and also males with somewhat different colouration also from Papua New Guinea These may represent a new species, though the possibility of sexual dimorphism in this group cannot be ruled out. Nothing is known of their biology though one species has been collected amongst mangroves (*Rhizophora*) in north Queensland, and other specimens have been collected in the Northern Territory, Victoria and Western Australia.

Testudobracon Quicke
(Figs 116-120)

Small wasps belonging to the Braconini. Only a few species have been described but we are aware of many undescribed ones from both Africa and the Indo-Australian region. *Testudobracon* species are apparently specialist ectoparasitoids of gall-forming, cecidomyiid Diptera, especially — and perhaps exclusively — Asphondylini (Quicke 1986a; Maetô, 1991). This is also partly confirmed by an Australian host record for the genus, based on an apparently undescribed species represented in the QDPI collection, which had been reared from a gall on '*A. polycarpa*'.

Key to the species of *Testudobracon* (♀♀ only)

1. Median emargination of 6th metasomal tergite shallow and with rounded lateral margins (Fig. 120); ovipositor (exserted part) at least 0.75 times length of forewing; precoxal suture (if distinguishable), represented by a week, complete, narrow, longitudinal groove 2
   - Median emargination of 6th metasomal tergite deep and with sharply defined (angular) lateral margins (Figs 117, 118); ovipositor (exserted part) less than 0.75 times length of forewing; precoxal suture present as a deep, smooth, rounded pit 3
2. Hind leg almost entirely pale yellow-brown; metasomal tergites 4-6 largely whitish, except for basal (anterior) third which is yellowish and postero-lateral lobes which are somewhat darker; vertex with distinct fine transverse, striate sculpture; metasomal tergites 4-6 rugulose ..... *T. longicaudis* Maetô
   - Hind leg almost entirely black; metasomal tergites 4-6 with basal (anterior) half black or piceous brown, and posterior half white; vertex totally smooth and shiny; metasomal tergites 4-6 irregularly punctate (Fig. 120) ..... *T. australicolorus* sp.nov.
3. Postero-lateral margin of 6th metasomal tergite with a pointed protuberance (Fig. 116) 4
   - Postero-lateral margin of 6th metasomal tergite with a rounded lobe-like protuberance (Fig. 119) 5
4. Middle lobe of mesoscutum largely glabrous except for line of notauli; body and legs virtually entirely brownish yellow ..... *T. unicolorus* sp.nov.
   - Middle lobe of mesoscutum largely setose (except for anterior face); body and legs commonly with black or piceous markings especially frons, vertex, part of mesopleuron, metanotum and propodeum, middle coxae and hind coxa and hind femur ..... *T. pleuralis* (Ashmead)
5. Body and legs (except telotarsi) entirely pale brownish yellow; postero-lateral margin of 6th metasomal tergite hardly produced ..... *T. tatyanae* sp.nov.
   - Body and hind legs extensively marked with black and dark reddish-brown, metasoma with obvious pattern of dark red, black and white ..... *T. niger* Quicke

Testudobracon australicolorus sp.nov.
(Fig. 120)

MATERIAL EXAMINED

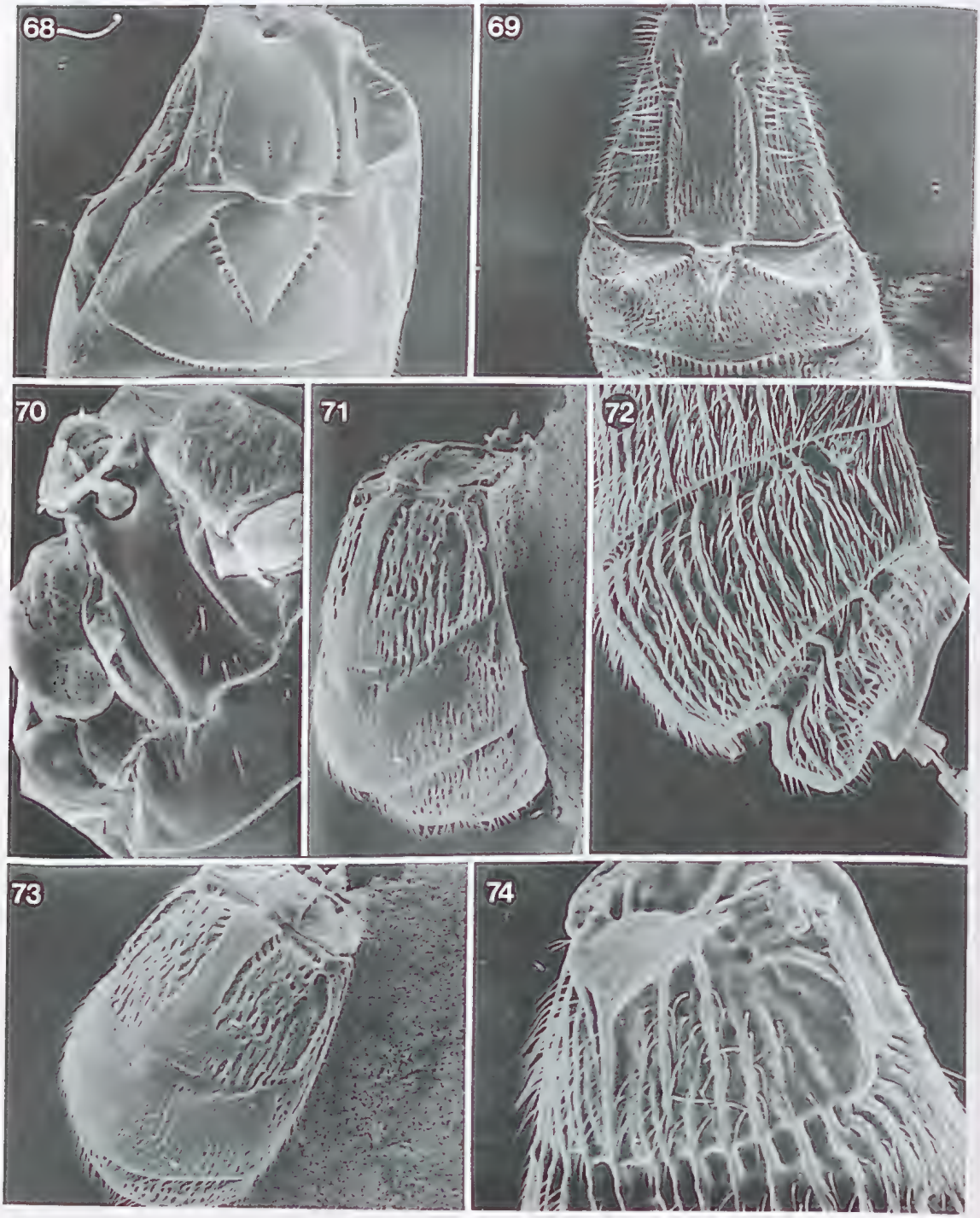
HOLOTYPE: ♀ with following labels: 'Mackay Queensland 1909-45', '834' & 'Mackay 3.92'. In collection of BMNH.

DESCRIPTION (♀)

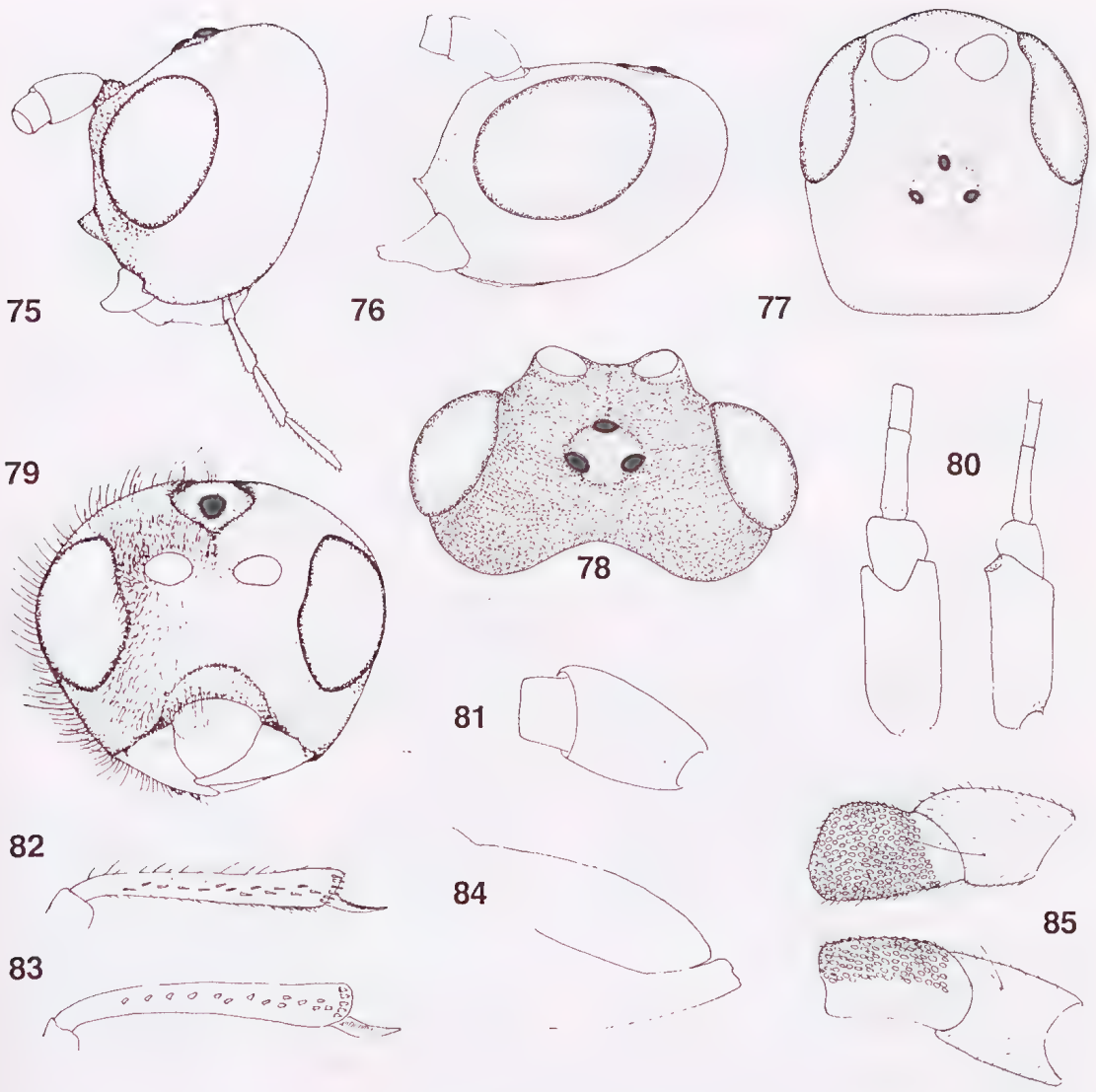
Length of body 3.7mm, of forewing 3.6mm and of ovipositor (part exserted beyond apex of metasoma) 2.9mm.

First flagellomere 1.1 times longer than both the 2nd and 3rd separately, the latter being 1.8 times longer than wide. Height of clypeus: intertentorial distance: tentorio-ocular distance = 1.0:2.2:1.58. Malar space 0.23 times height of eye. Face smooth and shiny medially, finely coriaceous laterally, without an obvious mid-longitudinal ridge. Height of eye: width of face: width of head = 1.0:1.1:2.1. Eyes sparsely short setose. Frons finely coriaceous medially, smooth and shiny laterally. Shortest distance between posterior ocelli: transverse diameter posterior ocellus: shortest distance between posterior ocellus and eye = 1.65: 1.0: 3.5. Horizontal length of eye 2.6 times horizontal length of head behind eye.

Mesoscutum smooth and shiny, setosity largely restricted to line of notauli. Precoxal suture rep-



FIGS 68-74. Features of the metasoma: 68, *Eunesaulax* sp., T1-T2; 69, *Chaoilta (Blastomorpha) decorata* Szépligeti, T1-T2; 70, *Myosoma* sp. (Indo-Australian), T1; 71, *Gelasinibracon* sp., T1-T5; 72, *Hyboteles* sp., T5- T6; 73, *Gelasinibracon* sp., T1-T3; 74, *Hyboteles* sp., T1.



FIGS 75-85. Features of head, mesosoma and legs: 75, *Ploceibracon monstrans* Quicke; 76, *Simplicibracon nigritarsus* sp.nov.; 77, *Atanycolus australiensis* sp.nov.; 78, *Pedinopleura australiensis* sp.nov.; 79, *Ploceibracon monstrans* Quicke; 80, *Atanycolus australiensis* sp.nov., base of antenna, dorso-lateral and dorsal aspects; 81, *Furcadesha walteri* sp.nov., scapus, lateral aspect; 82, *Atanycolus australiensis* sp.nov., fore tibia; 83, *Serratobracon cardaleae* Tobias, fore tibia; 84, *Atanycolus australiensis* sp.nov., profile mesoscutum and pronotum; 85, *Serratobracon cardaleae*, scapus and pedicellus, lateral and dorsal aspects.

resented by a complete but very weak, smooth, longitudinal groove.

Length of forewing veins SR1:3-SR:r = 5.2:2.8:1.0. Lengths of veins 2-SR:3-SR:r-m = 2.1:3.1:1.0.

Lengths of fore femur: tibia: tarsus = 1.05:1.0:1.2. Lengths of hind femur: tibia: basitarsus = 2.5:3.1:1.0. Hind tibia 5.7 times longer than wide.

Second metasomal tergite 2.7 times wider than medially long, with weak parallel-sided, smooth narrow median area, and with posteriorly converging, antero-lateral, longitudinal grooves nearly reaching posterior margin. Third tergite 2.9 times wider than medially long. Tergites 3 to 6 with weakly-developed, rounded postero-lateral lobes. Sixth tergite weakly emarginate me-

dially. Ovipositor approximately 0.8 times length of forewing.

Head, mesosoma fore and mid legs pale brownish orange except for piceous mark on top of head. Median parts of metasomal tergites 1-3 broadly brown to piceous, laterally whitish. Tergites 4-6 basally piceous brown, posteriorly white. Hind legs black. Wings pale brown with light to dark brown venation.

Testudobracon unicolorus sp.nov.
(Figs 116, 117)

MATERIAL EXAMINED
HOLOTYPE: ♀ with following labels: 'S.E. Queensland, Tamborine Mts. 19-26. iv. 1935' and 'AUSTRALIA: R.E.Turner B.M. 1935-240'. In BMNH collection.

DESCRIPTION (♀)
Length of body 2.6mm, of forewing 2.9mm and of ovipositor (part exserted beyond apex of metasoma) 1.7mm.

First flagellomere 1.2 and 1.4 times longer than the 2nd and 3rd respectively, the latter being 1.7 times longer than wide. Height of clypeus: intertentorial distance: tentorio-ocular distance = 1.0: 2.3: 1.7. Face largely finely coriaceous. Height of eye: width of face: width of head = 1.0:1.1:2.05. Eyes glabrous, not emarginate. Top of head shiny. Shortest distance between posterior ocelli: transverse diameter posterior ocellus: shortest distance between posterior ocellus and eye = 1.2: 1.0: 2.9. Horizontal length of eye 2.5 times horizontal length of head behind eye.

Mesosoma approximately as long as high. Notauli weak but distinct along whole length. Mesosutum setose medioposteriorly, along line of notauli and laterally. Precoxal suture represented by a deep pit.

Lengths of veins SR1:3-SR:r = 6.72: 2.5: 1.0. Lengths of veins 2- SR:3-SR:r-m = 1.25: 1.75: 1.0. Pterostigma 3.0 times longer than maximally wide.

Lengths of fore femur: tibia: tarsus = 1.0:1.0:1.27. Lengths of hind femur: hind tibia: hind basitarsus = 2.3:2.75:1.0. Hind tibia 6 times longer than maximally deep. Hind basitarsus 4.4 times longer than deep.

Second metasomal tergite 2.47 times wider than medially long; more or less uniformly foveate rugose, without mid-basal area and with only weak sub-lateral grooves anteriorly. Third tergite 2.57 times wider than medially long. Tergites 3-5 with well-developed, rounded, postero-lateral lobes. Tergite 6 postero-laterally with a pointed prominence and medially deeply semicircularly incised.

Uniformly pale brownish yellow except antennae and ovipositor sheaths which are black. Wings very pale brown with dark brown venation.

Testudobracon tatyanae sp.nov.
(Fig. 118)

MATERIAL EXAMINED
HOLOTYPE: ♀ with following labels: 'Mackay, Queensland. 1909-45.' and 'Mackay 1.01'. The type specimen is the right hand of two braconids glued to a single card square, in the BMNH collection.

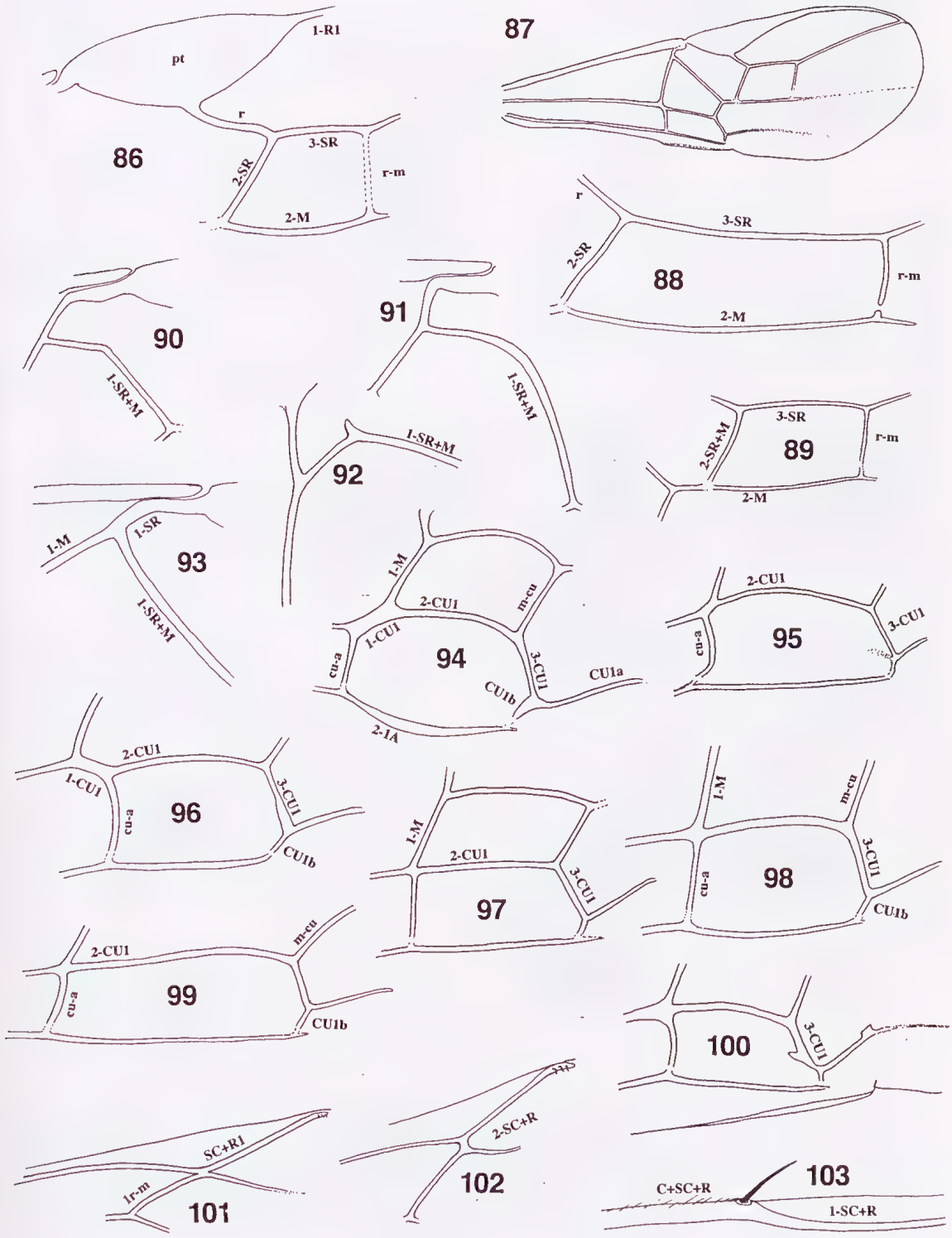
DESCRIPTION (♀)
Length of body 2.25mm, of forewing 2.9mm, of ovipositor (part exserted beyond apex of metasoma) 1.6mm, and of antenna 2.6mm [face not visible, glued on to card].

Antennae with 23 flagellomeres. Terminal flagellomere 2 times longer than wide. First flagellomere 1.1 times longer than both the 2nd and 3rd separately, the latter being 1.7 times longer than wide. Head very transverse. Horizontal length of eye 2.3 times longer than horizontal length of head behind eye. Vertex and temples smooth and shiny.

Mesosoma 1.15 times longer than high. Mesoscutum setose medio- posteriorly and along lines of notauli, otherwise smooth, shiny and glabrous. Precoxal suture represented by a smooth, deep, circular pit.

Lengths of forewing veins SR1:3-SR:r =

FIGS 86-103. Features of wing venation: 86, *Habrobracon* sp., pterostigma and 2nd submarginal cell; 87, *Trigastrotheca tricolor* sp.nov. 88-89, 2nd submarginal cell; 88, *Ligulibracon levor* Quicke; 89, *Furcadesha walteri* sp.nov. 90-93, forewing vein 1-SR+M: 90, *Vomeribracon* sp.; 91, *Calcaribracon willani* sp.nov.; 92, *Virgulibracon endoxylaphagus* sp.nov.; 93, *Stenobracon* sp. 94-100, 1st subdiscal cell: 94, *Cedilla cedilla* Quicke; 95, *Calcaribracon willani* sp.nov.; 96, *Euurobracon latitempus* Quicke; 97, *Eunesaulax terebrator* Tobias; 98, *Vipiellus* sp.; 99, *Paranesaulax* sp.nr. *nitor*; 100, *Ploceibracon monstrans* Quicke. 101-102, junction of hindwing veins 1r-m and SC+R1, to show orientation of 2-SC+R (between these): 101, *Gelasinibracon* sp.; 102, *Simplicibracon nigritarsus* sp.nov.; 103, *Atanycolus australiensis* sp.nov., apex of hindwing vein C+SC+R.


86
pt
1-R1
r
3-SR
2-SR
r-m
2-M
87
88
r
3-SR
2-SR
r-m
2-M
89
3-SR
2-SR+M
r-m
2-M
90
1-SR+M
91
1-SR+M
92
1-SR+M
93
1-M
1-SR
1-SR+M
94
1-M
2-CU1
m-cu
1-CU1
cu-a
3-CU1
CU1a
CU1b
2-1A
95
2-CU1
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3-CU1
96
2-CU1
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CU1b
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2-CU1
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101
SC+R1
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102
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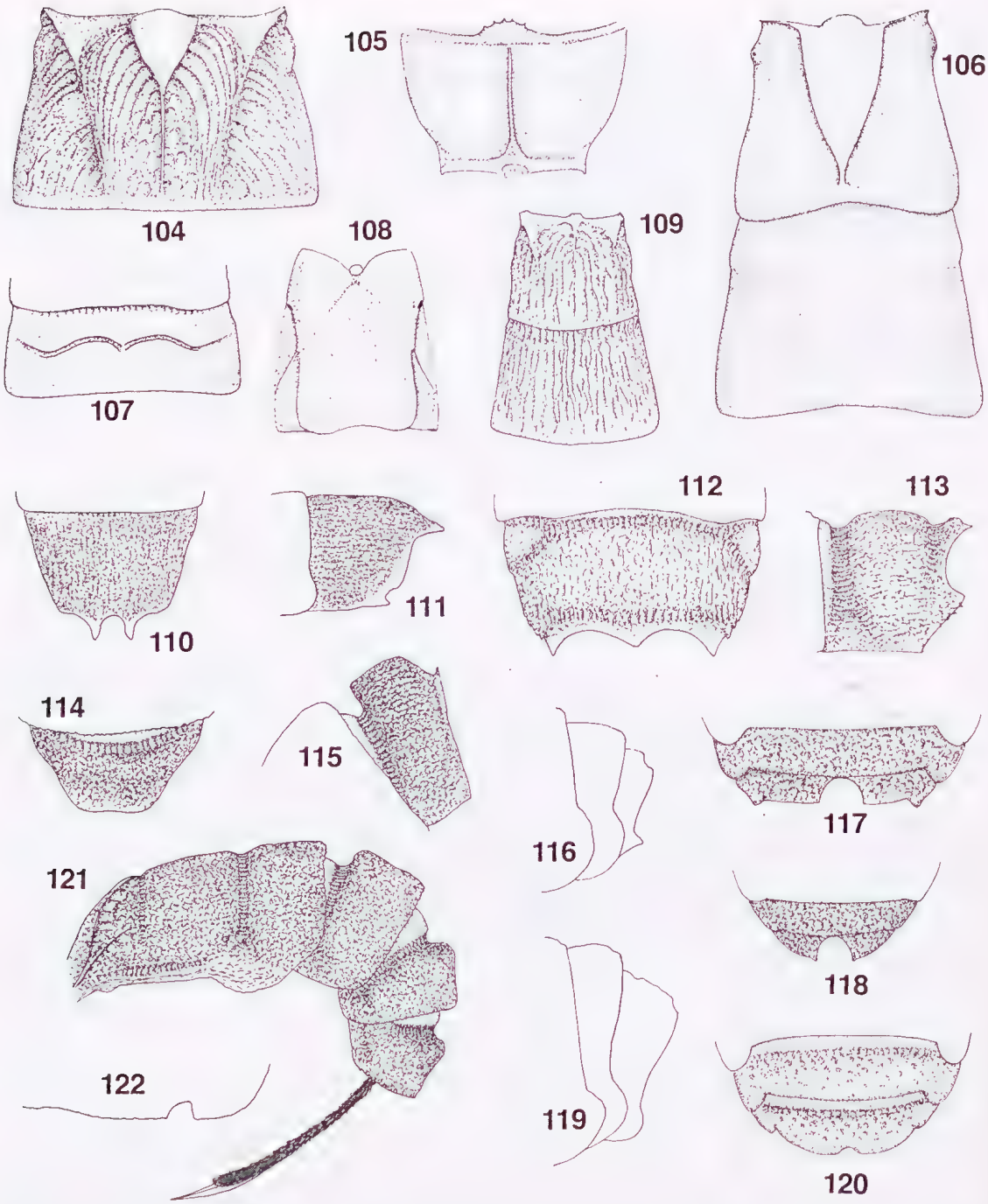
103
C+SC+R
1-SC+R



FIGS 104-122. Features of abdomen: 104, *Rostraulax xanthocephalus* (Turner), T2; 105, *Hyboteles toxopeusi* van Achterberg, propodeum; 106, *Paranesaulax* sp., T1-T2; 107, *Serratobracon cardaleae* Tobias, T3; 108 *Vomeribracon* sp., T1; 109, *Africadesha tobiasi* sp.nov., T2-T3; 110-111, *Furcadesha walteri* sp.nov., T5; 112-113, *Trigastrotheca tricolor* sp.nov., T5; 114, *Pedinopleura australiensis* sp.nov., T6; 115, *Hyboteles toxopeusi* van Achterberg, T6; 116, 117 *Testudobracon unicolorus* sp.nov., T5-T6; 118, *Testudobracon tatyanae* sp.nov., T5-T6; 119-120, *Testudobracon australicolorus* sp.nov., T5-T6; 121, *Pedinopleura australiensis* sp.nov.; 122, *Pedinopleura emarginata* van Achterberg, profile of lateral margin of syntergite T1-T3.

5.7:2.0:1.0. Lengths of veins 2-SR:3-SR:r-m = 1.47:1.53:1.0.

Lengths of fore femur: tibia: tarsus = 1.0: 1.05: 1.5. Lengths of hind femur:tibia:basitarsus = 2.8: 3.1: 1.0. Hind tibia 5.8 times longer than maximally deep. Hind basitarsus 3.8 times longer than deep.

Metasoma more elongate than typical *Testudobracon*. Second tergite 2.1 times wider than medially long; without mid-basal area but with moderately-developed sub-lateral grooves. Third tergite 2.25 times wider than medially long. Tergites 3 to 5 with very weak,, rounded postero-lateral lobes. Sixth tergite with a deep, semi-circular medial emargination.

Entirely pale brownish yellow except for antennae and ovipositor sheaths which are black and telotarsi which are slightly darkened. Wings weakly infuscate with brown venation.

ETYMOLOGY

Named after the senior author's wife Tanya for her tolerance of things hymenopterological.

*Trigastrotheca Cameron
(Figs 3, 13, 87, 112, 113)

Synonyms. *Coelodontus* Roman; *Odontopygia* Enderlein.

This is a small but widely-distributed genus originally described from Africa (*T. trilobata* Cameron) but is also known from India, the Philippines (Quicke, 1987b) and now Australia. Nothing is known of the biology of this group of Braconini though members of the closely related genus *Kenema* van Achterberg have been collected on several occasions from fields of grain crops.

Key to non-African species of *Trigastrotheca* (♀♀ only)

1. Forewing vein 3-SR more than 1.4 times longer than vein r-m; mesosoma uniformly orange; 2nd metasomal tergite unicolorous, ivory white; 3rd to 5th metasomal tergites orange .*T. tricolor* sp.nov.
- Forewing vein 3-SR less than 1.25 times longer than vein r-m; mesosoma black, marked with ivory white; 2nd metasomal tergite black medially, white laterally; 3rd to 4th metasomal tergites largely black, 5th ivory white ....*T. tridentata* (Enderlein)

Trigastrotheca tricolor sp.nov.
(Figs 3, 87, 112, 113)

MATERIAL EXAMINED

HOLOTYPE: ♀ with following labels: '7-14m. W. of Herberton, via Watsonville' and 'N. Queensland. 1 May 1967 D.H. Colless'. In ANIC collection.

PARATYPE: ♀ with same data as holotype. ANIC.

DESCRIPTION (♀♀)

Length of body 4.1mm, of forewing 4.2mm and of ovipositor (part exserted beyond apex of metasoma) 1.3mm.

Antenna with 40 flagellomeres. Terminal flagellomere acuminate, 2.1 times longer than wide. Penultimate flagellomere 1.3 times longer than wide. Median flagellomeres 1.3 times longer than wide. First flagellomere as long as the 2nd and 3rd separately, the latter 1.7 times longer than wide. Height of clypeus: inter- tentorial distance: tentorio-ocular distance = 1.0: 2.5: 2.0. Face finely punctate to coriaceous, otherwise shiny. Malar suture narrow but well-developed. Height of eye: width of face: width of head = 1.0: 1.2: 2.3. Frons flat without a mid-longitudinal ridge or lamella. Top of head finely coriaceous. shortest distance between posterior ocelli: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.3:1.0:2.5.

Mesosoma 1.46 times longer than high, largely with punctate sculpture on background of punctulate sculpture. Pronotum with finely crenulate groove. Notauli distinctly impressed along whole length of mesoscutum. Pre-scutellar sulcus narrow, with 6-7 crenulae. Scutellum rather flat, with reduced sculpture. Precoxal suture weak. Posterior margin of propodeum crenulate.

Forewing. Lengths of veins SR1:3-SR:r = 5.5:2.05:1.0. Lengths of veins 2-SR:3-SR:r-m = 1.15:1.5:1.0. Vein r issuing approximately 0.4 distance from base pterostigma. Vein 2-SR+M long, 0.3 times length of 2-M. Vein cu-a interstitial, straight, perpendicular.

Hindwing. Apex of vein C+SC+R with one especially thickened bristle. Base of wing with a glabrous area.

Claws with rounded basal lobes. Length of fore femur: tibia: tarsus = 1.0: 1.1: 1.2. Length of hind femur: tibia: basitarsus = 2.2: 3.0: 1.0. Hind tibia moderately slender without an obvious longitudinal, lateral groove.

Metasomal tergites 1-5 foveate rugose. Tergite 1 with ill-defined dorsal carinae. Tergites 3-5 with well-developed antero-lateral areas. Ovipositor (part extending beyond apex of meta-

soma) approximately 0.3 times length of forewing.

Largely yellow-brown (ochreous) except for the following: antennae black; head piceous brown with palps, labio-maxillary complex, labrum, mandibles except apex and two large, sub- rectangular areas laterally on the frons to temple area, pinkish ivory; two lines along the notauli, the posterior half of the middle lobe of the mesoscutum and the scutellum paler ochreous than remainder of mesosoma; propleuron piceous brown; mid- and posterior legs piceous brown with the junction between femur and tibia, and the tarsi paler brown; first and second metasomal tergites, the antenno-lateral areas of the third tergite and a narrow posterior margin of the two semi-circular emarginations of the fifth tergite, ivory white; postero-lateral corners of fifth tergite piceous; ovipositor sheaths black. Wings pale brown, slightly darker apically; venation dark brown except extreme base of pterostigma which is whitish.

Tropobracon Cameron
(Figs 15, 59)

Synonym: *Shirakia* Viereck

Small species of Braconini distributed from Australia (Queensland) to India and Africa and also occurring in the Palaearctic Region (China). Elsewhere, *Tropobracon* species have frequently been reared from pyralid moth larvae boring in stems of grain crops including rice. The occurrence of the genus in Australia was noted by Quicke (1988b).

Undabracon Quicke
(Fig. 125)

A small genus of small to medium-sized Aphrastobraconini. Only two species have been described, *U. nigrithorax* Quicke from Australia and *U. sinuatus* (Baltazar) from the Philippines' though we have seen two other undescribed species from Australia. Nothing is known of the biology of *Undabracon* though they are apparently nocturnal or crepuscular in habit (Quicke, 1992). Their arched ovipositor is reminiscent of that of another braconine genus, *Zaglyptogastra* Ashmead, which includes Afrotropical species that attack twig-boring cerambycid beetle larvae, probably through frass holes (Quicke, 1991b). One Australian species has been observed flying near fallen wood.

Vipiellus Roman
(Figs 25, 98)

The species of *Vipiellus* are small to medium-sized braconines found only in Australia. *Vipiellus* is closely related to the genera of Aphrastobraconini though it typically lacks the distinctive thickening of forewing vein CU1b. Species of *Vipiellus* have been reared several times from stem- boring xyloryctid larvae (Lepidoptera) including the macadamia twig-girdler, *Neodrepta luteotactella* (Walker).

*__Vipiomorpha__ Tobias
(Fig. 16)

Although *Vipiomorpha* was originally described on the basis of a Russian species, *V. ypsilon* Tobias, apparently congeneric species occur in Africa and Australia. *Vipiomorpha* spp. are rather small members of the Glyptomorphini and are the only representatives of that tribe so far found in Australia; we know of a large number of undescribed species. Within the Glyptomorphini, *Vipiomorpha* is rather unspecialized and is probably fairly close to the basal stock of that tribe. Nothing is known of the biology of *Vipiomorpha* but other Glyptomorphini are predominantly parasitoids of concealed Coleoptera larvae.

Virgulibracon Quicke
(Figs 19, 65, 92, 137, 138)

Virgulibracon is a small genus of large, entirely Australian wasps. Nothing is known of the biology of the type- species, *Virgulibracon vulsus* Quicke. However, *V. endoxylaphagus* sp.nov., is a common and widespread species that parasitizes larvae of the cossid moth *Endoxyla* (=*Xyleutes* of Authors), which bores in *Eucalyptus* trunks and branches (see above). We have seen specimens of apparently the same species from all over Australia but, because some differences in coloration have been observed, it is possible that there may be several similar species involved. In addi-

FIGS 123-138. Features of the ovipositor: 123, *Ligulibracon* sp.; 124, *Cedilla cedilla* Quicke; 125, *Undabracon* sp.; 126, *Curriea* sp.; 127, *Paranesaulax* sp.; 128, *Hybogaster* sp.; 129, *Iphiaulax* sp.; 130, *Pycnobraconoides froggattii* (Cameron) n. comb. 131, *Stigmatobracon* sp. 132, *Psittacibracon lacteolus* Quicke; 133, *Mollibracon bimaris* (Turner); 134, *Africadesha tobiasi* sp.nov.; 135, *Eunesaulax terebratus* Tobias; 136, *Eunesaulax* sp.; 137, 138, *Virgulibracon endoxylaphagus* sp.nov., paratype, lower valves retracted.

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tion, several other undescribed species vary in the number of hamuli on hindwing vein C+SC+R, wing and metasomal coloration and the development of a spur from forewing vein 3-CU1. These wasps bore through solid wood to a depth of more than 4cm to reach their hosts (see van Achterberg, 1986).

Key to species of *Virgulibracon*

1. Metasoma, fore and mid legs and pterostigma entirely black; ovipositor (part exserted beyond apex of metasoma) less than 2.25 times longer than forewing ..... *V. vulsus* Quicke
- Metasomal tergites 1-3 (at least) fore and mid legs and pterostigma orange to brownish orange; ovipositor (part exserted beyond apex of metasoma) more than 2.35 times length of forewing ..... *V. endoxylaphagus* sp.nov.

Virgulibracon endoxylaphagus sp.nov.
(Figs 19, 92, 137, 138)

MATERIAL EXAMINED

HOLOTYPE: ♀ with following data label: 'St Lucia, S.E. Queensland 8 Sep 1990. Ovipositing into *Endoxyla* (=*Xyleutes* of Authors) *cinereus* prepupa'. Deposited in QMBA.

PARATYPES: 3♀♀ with same data as holotype. 2♀ and 11♂ paratypes with following data label: 'St Lucia S.E. Queensland. 1 Sep 1990, G.B. Monteith. Emerging from Xyleutes Hole in 6' *Eucalyptus tereticornis* at 9.00 am'. All in QMBA except 1♀ and 1♂ in Quicke Collection, Sheffield.

DESCRIPTION (♀♀)

Length of body. 14.5-16.5mm, of forewing 16.0-17.0mm and of ovipositor 41-47mm.

Antenna with approximately 95 flagellomeres. Terminal flagellomere partly fused to the penultimate flagellomere. First flagellomere 1.5 and 1.8 times longer than the 2nd and 3rd flagellomeres respectively. 3rd flagellomere approximately as long as wide. Malar area shallowly depressed, finely coriaceous. Height of clypeus: inter-tentorial distance: tentorio-ocular distance = 1.0:6.0:3.8; clypeus without a transverse median carina, the lower part curved inwards to form roof of hypoclypeal depression. Face shiny with some punctuation. Height of eye: width of face: width of head = 1.0:1.36:2.5. Face 2.27 times wider than high. Frons weakly impressed with a deep mid-longitudinal sulcus. Shortest distance between posterior ocelli: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.5:1.0:2.75. Length of head behind eye: horizontal length of eye = 1.0:1.82.

Mesosoma approximately 1.47 times longer than high. Mesopleuron largely setose. Scutellar sulcus finely crenulate.

Forewing. Lengths of veins SR1:3-SR:r = 7.7:4.6:1.0. Lengths of veins 2-SR:3-SR:r-m = 1.37:2.8:1.0. Vein 1-SR+M with well- developed spur. Vein cu-a marginally postfurcal. Vein 3-CU1 weakly expanded posteriorly. Vein CU1a with a small anteriorly directed spur near its apex.

Hindwing. Vein 2-SC+R. Apex of vein C+SC+R with one especially thickened bristle. Vein R1 with 3 or 4 proper hamules. Base of wing with a large glabrous area.

Lengths of fore femur: tibia: tarsus = 1.0:1.2:1.1. Lengths of hind femur: tibia: basitarsus = 1.52:2.65:1.0. Hind tibia slender; with a distinct longitudinal lateral groove. Hind basitarsus 9.2 times longer than deep.

Metasoma smooth and shiny. Antero-lateral parts of 2nd tergite and posterior margins of 3rd to 7th tergites membranous. Second tergite 1.3 times wider posteriorly than medially long. Ovipositor approximately 4 times longer than metasoma, 2.5 times longer than forewing.

Brown-orange except for the following which are black: antennae, mesosoma, hind legs, most of metasomal tergites 4-7, ovipositor sheaths. Membranous posterior margins of tergites 3-7 pinkish white. Basal third of wings pale yellowish, apical two thirds smoky; venation largely dark brown but C+SC+R and pterostigma orange.

DESCRIPTION (♂♂)

Males are smaller than females; body length 11-13mm.

Virgulibraconoides Quicke
(Fig. 4)

A medium-sized genus of medium-sized wasps, which has been previously confused with *Callibracon* (see e.g. Ashmead, 1900), although they are not closely related. Probably the majority of species, all of which appear to be Australian, are undescribed.

Vomeribracon Quicke
(Figs 66, 90,108)

A small genus of medium-sized to large wasps occurring in Australia (north Queensland) and Papua New Guinea. Nothing is known of the biology of the only Australian species, *V. ingres-*

sor (Turner). However, an undescribed species from Papua New Guinea is an important larval parasitoid of the curculionid, *Pantorytes szentivanyi*, which is an important pest of cocoa (G. Holloway, pers. comm.).

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THE TADPOLES OF TWO QUEENSLAND FROGS (ANURA: HYLIDAE, MYOBATRACHIDAE)

STEPHEN J. RICHARDS AND ROSS A. ALFORD

Richards, S.J. & Alford, R.A. 1993 06 30: The tadpoles of two Queensland frogs (Anura: Hylidae, Myobatrachidae). *Memoirs of the Queensland Museum* **33**(1): 337-340. Brisbane. ISSN 0079-8835.

The tadpoles of two Queensland frogs, *Cyclorana brevipes* and *Uperoleia mimula*, are described and illustrated. *C. brevipes* is similar to previously described *Cyclorana*, having a rotund body and a 2(2)/3(1) tooth row formula. *U. mimula* shares with *U. lithomoda* an extremely small oral disc, a tooth row formula of 2(2)/3, and a black tail tip. □ *tadpoles, Hylidae, Myobatrachidae, Cyclorana brevipes, Uperoleia mimula, Queensland.*

Stephen J. Richards and Ross A. Alford, Zoology Department, James Cook University, Queensland 4811, Australia; 11 November, 1992.

Despite increased interest in Queensland's anuran fauna, the larvae of many species remain unknown. Given current concern about the conservation status of many species (Tyler, 1991; Wyman, 1990), accurate identification of larvae is important. The ability to identify larvae simplifies determination of the distribution and abundance of species, and is necessary for elucidation of their ecologies and life histories.

During research on frog communities in savanna woodland near Townsville, we collected amplexing pairs of two frogs whose larvae were unknown: the hylid *Cyclorana brevipes* and the myobatrachid *Uperoleia mimula*. These frogs were returned to the laboratory where oviposition occurred and larvae were reared to metamorphosis. In this paper we describe and illustrate the tadpoles of these species.

METHODS

Amplectant frogs transported to the laboratory were placed in large glass aquaria with 2-3cm of water at 25°C. Oviposition occurred within 12 hrs. When *C. brevipes* embryos reached stage 23 (Gosner, 1960) they were placed in 1000 litre plastic cattle tanks on the James Cook University campus. These tanks were assembled as described by Hearnden (1992), and supported a complex aquatic community similar to those found in temporary pools in the Townsville area, but lacking other anurans and most predators. Water temperature in the tanks ranged from 20-34°C. *U. mimula* tadpoles were reared for several weeks under artificial conditions in the laboratory prior to placement in the tanks, so no attempt was made to estimate larval period for this species.

Preserved specimens were measured using a dissecting microscope with an eyepiece micrometer. Terminology follows Altig (1970) and McDiarmid & Altig (1989). All measurements are in millimetres. Measurements involving apertures were taken from the centre of the aperture. The staging system is that of Gosner (1960). Specimens are lodged in the tadpole collection of the Zoology Department, James Cook University.

Cyclorana brevipes
(Figs 1,2)

An amplexing pair was collected in a ditch at the intersection of Black River Road and Bruce Highway, 20km north of Townsville, Qld. on the evening of 2/3/90. Oviposition occurred before 0800 on 3/3/90 (n = 930 eggs), and embryos reached stage 23 by 5/3/90. The first metamorph (stage 46), observed on 28/3/90, measured 23.0mm snout to vent length and weighed 1.26g. The minimum total duration of development (fertilization to metamorphosis) was 25 days.

A stage 37 tadpole has the following measurements (millimetres): 56.0 total length, 22.5 body length, 4.5 basal tail muscle height, 3.5 basal tail muscle width, 2.8 maximum dorsal fin height located 10.8 from body terminus, 2.5 maximum ventral fin height located 11.0 from body terminus, 11.8 maximum body width, 10.8 maximum body height, 2.5 eye diameter, 0.9 pupil diameter, 7.2 interorbital distance, 0.5 × 0.3 narial diameters, 2.9 internarial distance, 3.2 snout-naris, 6.4 snout-eye, 11.8 snout-spiracle, 3.3 naris-eye, and 5.4 transverse oral disc diameter.

The oral disc is anteroventral and non-emarginate. The marginal papillae are in a single row

ventrally, with a wide gap dorsally and additional submarginal papillae laterally and dorsolaterally. The labial tooth row formula is 2(2)/3(1). The jaw sheaths are keratinized, the lower jaw sheath broad and V-shaped, and the upper jaw sheath narrow and curved (Fig. 1). The serrations on the margin of the upper jaw sheath are much finer than those on the lower jaw sheath.

The body is rotund, the snout is rounded in dorsal view, and the eyes are dorsolateral. The nares are dorsal and oriented anterolaterally. The sinistral spiracle is short and unpigmented, is almost ventral, and is not visible in dorsal view. The vent tube is short and dextral. The dorsal fin is not arched, and tapers to a narrow point posteriorly. It originates slightly anterior to the junction of the body and the tail musculature (Fig. 2). Dark pigmentation deep in the skin layers covers the intestinal coil dorsolaterally, from a line just posterior to the eyes. Lighter, diffuse brown pigment occurs on the rest of the body, tail muscle and fins. A patch of darker pigmentation almost surrounds the nares, with a lateral gap.

Uperoleia mimula
(Figs 3,4)

An amplexing pair was captured at an overflow area of a small creek near Bentley Dam, approximately 20km south of Townsville, in March 1990. A stage 38 specimen has the following measurements: 20.2 total length, 10.0 body length, 2.3 basal tail muscle height, 1.7 basal tail muscle width, 1.9 maximum dorsal fin height located 3.8 from body terminus, 1.3 maximum ventral fin height located 4.8 from body terminus, 6.6 maximum body width, 5.4 maximum body height, 1.4 eye diameter, 0.4 pupil diameter, 2.9 interorbital distance, 0.4 narial diameter, 1.3 internarial distance, 1.1 snout-naris, 2.4 snout-eye, 8.0 snout-spiracle, 1.4 naris-eye, 1.6 transverse oral disc diameter.

The oral disc is extremely small, located anteroventrally, and is non-emarginate. The jaw sheaths are narrow and keratinized. The labial tooth row formula is 2(2)/3. The short P3 tooth row is supported on an unusual flexible flap. Large marginal papillae in a single row surround the disc, with a large anterior gap and a narrow posterior gap (Fig. 3). The snout is rounded in dorsal view and the eyes are dorsal. The nares are located dorsally and open almost verically.

The body is slightly flattened dorsoventrally, and is oval when viewed from above. The spiracle is sinistral, located laterally and near the posterior of the body. It is extremely short, lightly pigmented, and oriented posteriorly (Fig. 4). The anus is dextral. Diffuse brown pigment occurs on the dorsal and lateral surfaces of the body, and on the tail muscle. Pigmentation on the fins is concentrated at the posterior tip in tadpoles that have not reached stage 31, forming a conspicuous black 'flag' that occupies approximately the most posterior 15-20% of the tail. From about stage 31 the pigment gradually disperses, until at stage 36 the 'flag' is hardly visible.

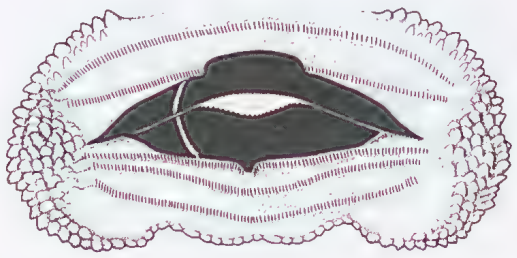

FIG. 1. Oral disc of *Cyclorana brevipes*. Scale bar = 1mm.

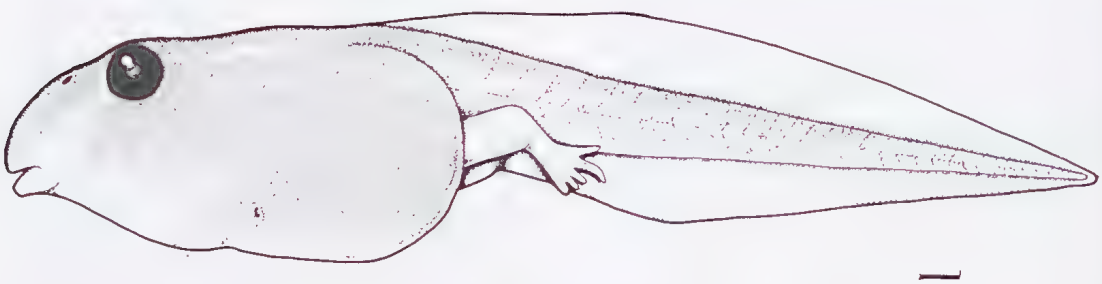

FIG. 2. Lateral view of a stage 37 *Cyclorana brevipes*. Scale bar = 2mm.

DISCUSSION

The tadpole of *Cyclorana brevipes* is difficult to distinguish from other *Cyclorana* previously described (Tyler & Martin, 1975; Tyler et al., 1982; Tyler et al., 1983; Watson & Martin, 1973). All have rotund bodies, tooth row formulae of 2(2)/3(1), and similar configurations of oral papillae. Tyler et al. (1983) were unable to distinguish tadpoles of *C. australis* from *C. longipes* when they occured together in ponds in the Northern Territory, until the distinctive dorsal pattern of *C. longipes* appeared near metamorphosis. The tadpoles of these species reached different maximum sizes, but this character is only useful if late stage tadpoles are available for comparison.

Because of the extreme morphological conservativism displayed by this genus, accurate identification of Queensland tadpoles can best be achieved by the construction of regional keys that compare only the species found in a given area. The similarities in oral morphology exhibited by *Cyclorana* tadpoles will make knowledge about colour in life (and in preservative), and about size differences during development, fundamental for accurate identification. Knowledge about Queensland *Cyclorana* is insufficient for such keys to be constructed at this stage.

Over 20 species of *Uperoleia* are now known to occur in Australia (Davies et al., 1986). However, information on the larval morphology of *Uperoleia* species is available for only four species, so meanigful comparisons are difficult. Two species, *U. inundata* (Tyler et al., 1983) and *U. lithomoda* (Davies et al., 1986) share with *U. mimula* a tooth row formula of 2(2)/3. *U. lithomoda* also shares with *U. mimula* a black tail tip. *U. laevigata* (as *U. marmorata*) is reported to lack gaps in any of the toothrows and has a formula of 1/3 (Moore, 1961). *U. tyleri* (as *U. marmorata*) differs from *mimula* in having a gap in the P1 tooth row (Watson & Martin, 1973).

None of these authors mention the unusual flap supporting the P3 tooth row. However the illustration of *U. inundata* in Tyler et al. (1983) suggests that this structure may be present in that species, and careful examination of other species may reveal its presence. The morphology and function of this structure require further study, as does the possibilty that it may be a generically diagnostic feature.

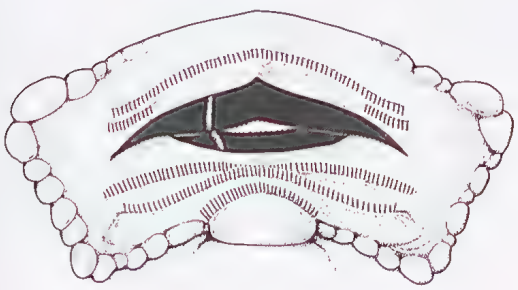

FIG. 3. Oral disc of *Uperoleia mimula*. Scale bar = 2mm.

ACKNOWLEDGEMENTS

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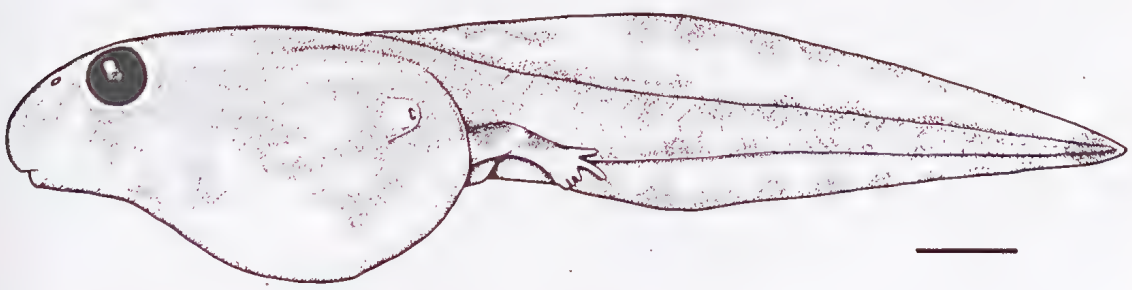

FIG. 4. Lateral view of a stage 38 *Uperoleia mimula*. Scale bar = 2mm.

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A NEW TWO-TOED SKINK FROM EASTERN AUSTRALIA

G.J. INGRAM, P.J. COUPER AND S.C. DONNELLAN

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Lerista emmotti sp.nov. has been confused with *L. punctatovittata* (Günther, 1867). However, it differs from *L. punctatovittata* in the state of the forelimb (distinctly didactyle vs monodactyle or monostylus). As well, it can be distinguished by estimates of genetic distance derived from allozyme electrophoresis. □ *Scincidae, Lerista emmotti, Lerista punctatovittata, new species, electrophoresis, Australia.*

Glen Ingram & Patrick Couper, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; Steve Donnellan, Evolutionary Biology Unit, South Australian Museum, North Terrace, Adelaide, South Australia 5000, Australia; 30 April, 1993.

When Couper & Ingram (1992) described *Lerista colliveri*, they were aware of another probable species of *Lerista* that had been confused with *L. punctatovittata*. It differed in the state of the forelimb (distinctly didactyle vs monodactyle or monostylus). However, no other morphological characteristics that differentiated them were found. As well, the different states of the limb did not appear to be a good enough reason to describe a new species. Degenerate-limbed skinks may vary in the extent of development of the toes, and the different conditions are more valuable in the study of embryology than as characters for differentiating taxa. However, subsequent work by one of us (SCD) showed that the two-toed individuals could be distinguished by estimates of genetic distance derived from allozyme electrophoresis.

Queensland Museum's specimens are prefixed by QMJ, Australian Museum's by AMR and South Australian Museum's by SAMAR.

ELECTROPHORESIS

Materials and Methods

Twenty-seven '*Lerista punctatovittata*' were collected from 11 localities in Queensland, New South Wales and South Australia. Livers were dissected from fresh specimens and stored at -80°C until use. For the genetic analysis, specimens from a single locality which showed all the expected genotypes at each locus were treated as a population of a single genetic type. On this basis, 11 populations were designated:

Noon – Noonbah Station, Qld (24°07'S, 143°11'E) (QMJ54144-6);

Ston – Waterloo Station, via Stonehenge, Qld (24°16'E, 143°17') (QMJ56312-4);

Kaka – Ka Ka Mundi, Qld (24°49'E, 147°24'S) (QMJ56090);

Nyma – Nymagee, NSW (32°01'E, 146°20S) (SAMAR33548-50/552-7);

Mtho – Mt Hope, NSW (32°51'E, 145°53'S) (SAMAR33522);

Chow – Chowilla, SA (33°56'E, 140°59'E) (SAMAR32991-2, 33003);

Poog – Pooginook CP, SA (34°04'E, 140°07'S) (SAMAR38345/352);

Waik – 2km S Waikerie, SA (34°12'E, 140°01'S) (SAMAR39731);

Broo – Brookfield CP, SA (34°19'E, 139°30'S) (SAMAR36974);

Wida – 11km S Widara HS, SA (34°20'E, 139°57'S) (SAMAR38442)

Boon – 4.5km E Boongalechie, SA (34°27;'S, 139°26'E) (SAMAR39267).

Homogenates of liver were electrophoresed on sheets of cellulose acetate (Cellogel: Chemetron) as described by Richardson et al. (1986), and were assayed for 35 enzymes which were encoded by 40 presumptive loci. The enzymes stained, E.C. numbers and abbreviations (Murphy et al., 1990) are: aspartate aminotransferase (AAT, E.C. 2.6.1.1), aconitate hydratase (ACOH, E.C. 4.2.1.3), aminoacylase (ACYC, E.C. 3.5.1.14), alcohol dehydrogenase (ADH, E.C. 1.1.1.1), adenylate kinase (AK, E.C. 2.7.4.3), alanine aminotransferase (ALAT, E.C. 2.6.1.2), carbonate dehydratase (CA, E.C. 4.2.1.1), leucine aminopeptidase (CAP, E.C. 3.4.11.1), enolase (ENO, E.C. 4.2.1.11), fructose-diphosphatase (FBP, E.C. 3.1.3.11), fumarate hydratase (FUMH, E.C.4.2.1.2), glyceraldehyde-phosphate dehydrogenase (GAPDH, E.C. 1.2.1.2), guanine deaminase (GDA, E.C. 3.5.4.3), glycerol-3-phosphate dehydrogenase (G3PDH, E.C. 1.1.1.8), glucose-6-phosphate dehydrogenase (G6PDH, E.C. 1.1.1.49), glucose-phosphate isomerase (GPI, E.C. 5.3.1.9), glutathione reductase (GR, E.C. 1.6.4.2), glutamate dehydrogenase (GTDH, E.C. 1.4.1.3), L-iditol dehydrogenase (IDDH, E.C. 1.1.1.14), isocitrate dehydrogenase (IDH, E.C.

TABLE 1. Electromorph frequencies, expressed as a percentage, in 11 populations of '*Lerista punctatovittata*' at 40 loci. Electromorphs are designated alphabetically, with 'a' being the most cathodally migrating electromorph. Where enzymes are encoded by more than one locus, the loci are designated numerically in order of increasing electrophoretic mobility. Where the electromorph frequencies are not given, the frequency is 100. See 'Material and Methods' for an explanation of the population codes. The number of individuals sampled from each population is given under each locus. The following loci were invariant: *Aat-1, Aat-2, Acoh-1, Acyc, Adh, Ak-1, Ak-2, Ca, Cap, Eno, Fumh, Gapdh, Gda, G3pdh, Gpi, Gtdh,Iddh, Ldh-1, Ldh-2, Lgl, Mdh- 1, Mdh-2, Mpi, Pgam, Pk* and *Sod*.

LOCUS	STON	NOON	KAKA	MTHO	NYMA	CHOW	BROO	POOG	WIDA	BOON	WAIK
Acoh-2	e(50)	f(33)	d	d	d	d	d	d	d	d	d
	a(50)	c(17)									
		b(33)									
		a(17)									
	3	3	1	1	10	3	1	2	1	1	1
Alat	b	a	a	a	a	a	a	a	a	a	a
	2	3	1	1	10	3	1	2	1	1	1
Fbp	a	a	a	b	b	b	b	b	b	b	b
	3	3	1	1	10	3	1	2	1	1	1
G6pdh	b(17)	b(33)	a	a	a	a	a	a	a	a	a
	a(83)	a(67)									
	3	3	1	1	10	3	1	2	1	1	1
Gr	a	b(50)	a	-	a	a	a	a	a	-	a
		a(50)									
	2	2	1	0	10	3	1	2	1		1
Idh	a	b(33)	a	b	b(35)	b(50)	b	b(50)	b	b	b(50)
		a(67)			a(65)	a(50)		a(50)			a(50)
	1	3	1	1	10	3	1	2	1	1	1
Mdhp	a	a	a	b	b(85)	b(67)	b(50)	b	b	b	b
					a(15)	a(33)	a(50)				
	3	3	1	1	10	3	1	1	1	1	1
PepA	b	b(50)	b	b	b(80)	b	b	b(75)	b	b	b
		a(50)			a(20)			a(25)			
	3	3	1	1	10	3	1	2	1	1	1
PepB	c(33)	b	b	b(50)	b	b(83)	b(50)	b	a	b(50)	b(50)
	b(67)			a(50)		a(17)	a(50)			a(50)	a(50)
	3	3	1	1	10	3	1	2	1	1	1
PepD	a	b	a	a	a	a	-	a	a	a	a
	3	2	1	1	10	3		1	1	1	1
Pgdh	b	a	b	b	b	b	-	b	b	b	b
	3	3	1	1	10	3		1	1	1	1
Pgm-1	a	b(67)	b	b	b(61)	b(67)	b(50)	b(50)	a	b(50)	b(50)
		a(33)			a(39)	a(33)	a(50)	a(50)		a(50)	a(50)
	3	3	1	1	9	3	1	1	1	1	1
Pgm-2	a	a	b(50)	a	a	a	a	a	a	a	a
			a(50)								
	3	3	1	1	10	3	1	2	1	1	1
Tpi	a	a	a	a	a	a	a	a	b(50)	a	a
									a(50)		
	3	3	1	1	10	3	1	2	1	1	1

1.1.1.42), lactate dehydrogenase (LDH, E.C. 1.1.1.27), lactoyl-glutathione lyase (LGL, E.C. 4.4.1.5), malate dehydrogenase (MDH, E.C. 1.1.1.37), 'malic' enzyme (MDHP, E.C. 1.1.1.40), mannose-phosphate isomerase (MPI, E.C. 5.3.1.8), peptidases (PEP, E.C. 3.4.11 or 13.*), phosphoglycerate mutase (PGAM, E.C. 5.4.2.1), 6-phosphogluconate dehydrogenase (PGDH, E.C. 1.1.1.44), phosphoglucomutase (PGM, E.C. 2.7.5.1), pyruvate kinase (PK, E.C. 2.7.1.40), superoxide dismutase (SOD, E.C. 1.15.1.1), and triose-phosphate isomerase (TPI, E.C. 5.3.1.1). Electromorphs were identified by comparison with samples that were repeatedly included on each gel (internal controls) and through critical side-by-side comparisons (line-ups; see Richardson et al., 1986).

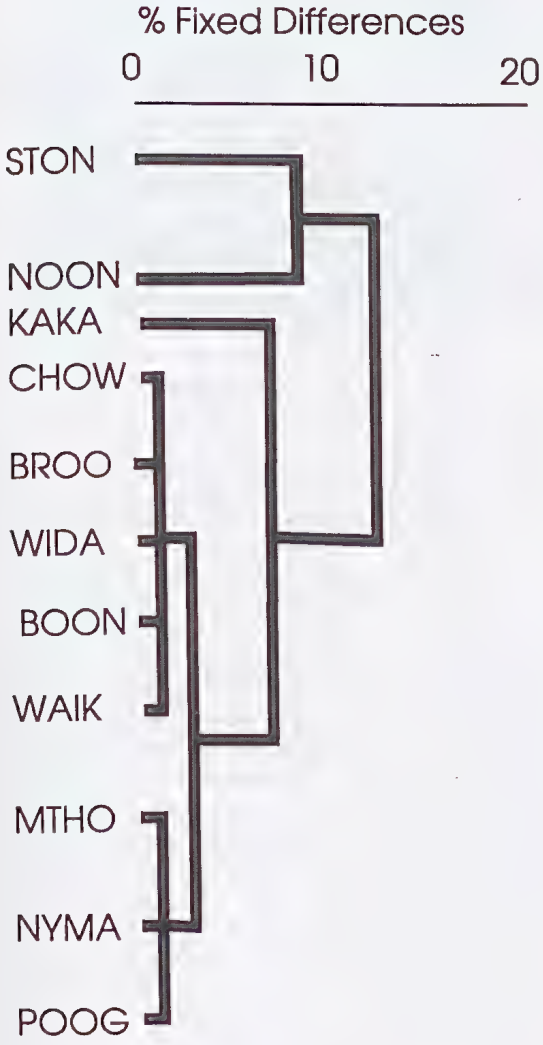

FIG. 1. Phenogram of the percentage fixed differences between populations, constructed by the unpaired group method of analysis (UPGMA).

RESULTS

Electromorph distributions at the 40 loci resolved are shown in Table 1. These data were converted into a matrix of percentages of loci showing fixed differences between populations (Table 2). A fixed difference occurs at a locus when the two populations being compared share no electromorphs (Richardson et al., 1986). Figure 1 is a phenogram of the percentage fixed differences between populations, constructed by the unpaired group method of analysis (UPGMA). The phenogram is not intended to reflect phylogenetic relationships, but rather to give a visual indication of the genetic diversity and genetic distances between the 11 populations. The specimens fell into three major genetic groups: 1, Stonehenge; 2, Noonbah; and 3, Ka Ka Mundi and the populations from NSW/SA.

The Stonehenge and Noonbah populations are regionally sympatric (separated by 15km) and have fixed differences at 3 loci (*Gpt, PepD* and *Pgdh*). The Ka Ka Mundi/NSW/SA populations have fixed differences with Stonehenge and Noonbah at a minimum of 3 (*Acoh-2*, *Alat* and *Fbp*) and 2 loci (*Acoh-2* and *Fbp*; *PepD* and *Pgdh* not scored in Brookfield population) respectively. Within the Ka Ka Mundi/NSW/SA group, Ka Ka Mundi has a single fixed difference (*Fbp*) with the NSW/SA populations.

From the preceding electrophoretic analysis, the Noonbah population is clearly distinct from the other populations. Morphologically, all the Noonbah specimens have a didactyl forelimb while the specimens from the other populations have a monodactyl or monostylar forelimb. The latter are identifiable with *L. punctatovittata* and the Noonbah specimens thus warrant recognition as members of a new species.

SYSTEMATICS

Lerista emmotti sp.nov.
(Figs 2-4)

1992 *Lerista punctatovittata* (in part); Cogger, 1992.

MATERIAL EXAMINED

HOLOTYPE: QMJ53959 Noonbah Stn, 140km S of Longreach (24°07'S, 143°11'E), CQ, A. Emmott, 2 September 1991.

FIG. 2. *Lerista emmotti* sp.nov., paratype QMJ51630 in life, Noonbah Station, CQ (Steve Wilson).

PARATYPES: QMJ9038 Muttaburra (22°36'S, 144°33'E), CQ; QMJ54491-2 Hickleton Stn (24°02'S, 143°08'E), CQ; QMJ50066, 50068-69, 51217-8, 51629-30, 52585-7, 53958, 53960, 54144-6, 54292, 54493 Noonbah Stn (24°07', 143°11'), CQ;QMJ 51529, no data; AMR92302 Wooltana Homestead (30°25'E, 139°25'S), SA; AMR14682, Mootwingee Water Holes (31°17'E, 142°18'S), NSW; AMR114408 north end of Mungo Homestead airstrip, Mungo NP (33°43'S, 142°57'E), NSW; AMR114314 Old Arumpo Homestead (33°48'S, 142°53'S), NSW.

DIAGNOSIS

A large (maximum snout-vent length 103mm) *Lerista* with a movable eyelid and didactyl fore- and hindlimbs. A member of the *L. macropisthopus* species group (cf. Wilson & Knowles, 1988), of which the following members may also be didactyle on both fore- and hindlimbs: *L. gerrardii*, *L. neander* and *L. picturata*. *L. emmotti* is readily distinguished from *L. gerrardii* by pattern (broad black upper lateral stripe absent vs broad black upper lateral stripe present); from *L. nean-*

TABLE 2. Matrix of percentage fixed allelic differences between 11 populations of '*Lerista punctatovittata*'.

	STON	NOON	KAKA	MTHO	NYMA	CHOW	BROO	POOG	WIDA	BOON	WAIK
STON	-										
NOON	8	-									
KAKA	8	8	-								
MTHO	15	13	8	-							
NYMA	8	10	3	0	-						
CHOW	8	10	3	0	0	-					
BROO	13	7	7	0	0	0	-				
POOG	10	13	5	0	0	0	0	-			
WIDA	15	15	14	3	3	0	0	3	-		
BOON	14	14	8	0	0	0	0	0	0	-	
WAIK	10	13	5	0	0	0	0	0	0	0	-

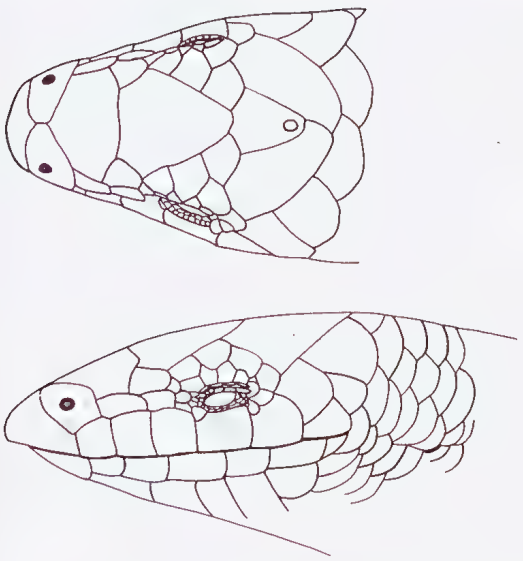

FIG. 3. *Lerista emmotti* sp.nov. (paratype QMJ51218). Above: dorsal view of head. Below: lateral view of head.

der by the number of supraciliaries (5 vs 3); from *L. picturata* by the number of supraciliaries (5 vs 1-3). *L. emmotti* most closely resembles *L. punctatovittata* but it can be separated from this species by the state of the forelimb (distinctly didactyle vs monodactyle or monostylus). *L. emmotti* is further distinguished from *L. punctatovittata* by the biochemical data in Table 1.

DESCRIPTION

Snout-vent length: 39-103mm (N 24, mean 72.6). Length of appendages etc. (% snout-vent length): forelimb 3-7 (N 24, mean 4.5), hindlimb 11-16 (N 24, mean 13.0), tail 87-122 (N 13, mean 105.2), head length 8-13 (N 24, mean 9.9), head width 6-9 (N 24, mean 6.9).

Nasal contact narrow (N 1) to moderate (N 20) to broad (N 5). Nostril positioned anteriorly to centrally on nasal scale. Rostral shield rounded in profile. Prefrontals small to moderate, widely spaced. Interparietal large and free. Frontoparietals narrowly (N 4) to moderately (N 22) spaced, smaller than interparietal. Parietals in narrow contact (N 1), moderate contact (N 3), broad contact (N 22). Enlarged nuchal scales 5-9 (N 14, mean 7.8), of which only two contact the parietals. Lower eyelid movable. Opaque disc occupying more than half the lower eyelid. Supraoculars 3, first two in contact with the frontal. Supraciliaries 5 (N 26). Loreals 2, second usually smaller. Presuboculars 2. Supralabials 6, fourth below eye. Infralabials 5-6 (N 26, mean 5.9). Primary temporals 1. Secondary temporals 2, lower smallest and overlapping upper. Ear aperture minute, overlapped by scales. Midbody scale rows 18, rarely 20 (N 26, mean 18.3). Paravertebral scales 78-90 (N 24, mean 85.5). Two enlarged preanal scales (N 25); right overlapping left (N 14), left overlapping right (N 11). Forelimb with two digits; both digits clawed (N 19), only one digit clawed (N 6), neither digit clawed (N 1). Hindlimb with two clawed digits, 2nd digit markedly longer than 1st. Lamellae under longest toe 9-12 (N 26, mean 10.6).

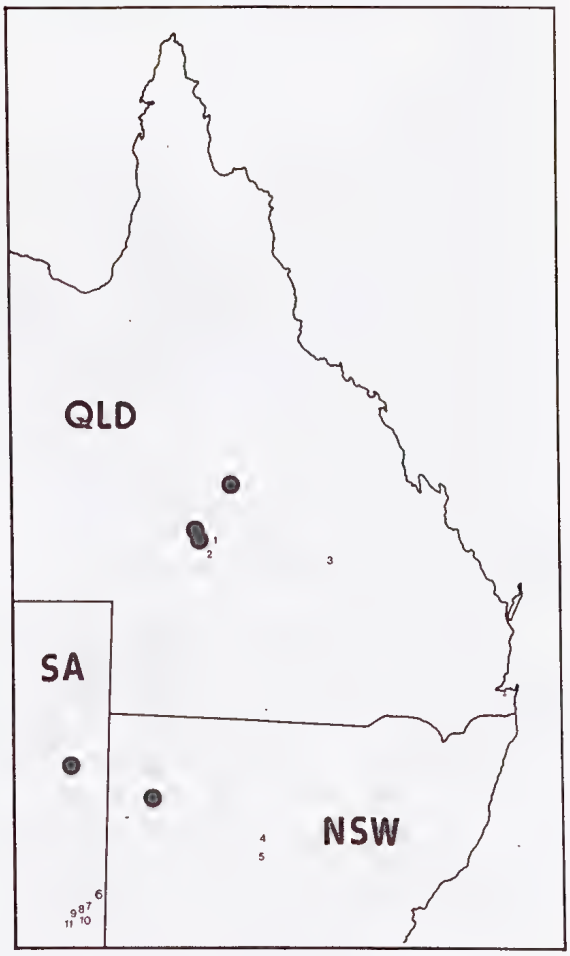

FIG. 4. Distribution of *Lerista emmotti* sp.nov. Numbers refer to populations of '*L. punctatovittata*' electrophoresed: 1, Noon; 2, Ston; 3, Kaka; 4, Nyma; 5, Mtho; 6, Chow; 7, Poog; 8, Waik; 9, Broo; 10, Wida; 11, Boon.

Dorsal and upper lateral ground colour tan to mid-brown with the each scale bearing a dark streak, which in turn form longitudinal lines of dark spots. Mid to lower lateral zone cream, marked by dark flecks. Venter either immaculate cream, or sometimes obscurely marked by dark-edged scales. Under surface of tail faintly to strongly patterned with dark flecks. Head shields dark-edged; lips barred; loreals and temporals marked by a dark streak which breaks up posteriorly.

DISTRIBUTION

From Muttaburra (22°36'E, 144°33'S), central Queensland, southwest to old Arumpo homestead, (33°48'E, 142°53'S), New South Wales. Also extending into South Australia (30°25'E, 139°25'S).

ETYMOLOGY

Named for Angus Emmott, naturalist and friend of the Queensland Museum.

REMARKS

Our examination of the holdings of the Queensland and Australian Museums showed '*L. punctatovittata*-like' *Lerista* with didactyl forelimbs to be confined to the western edge of the known distribution of *L. punctatovittata*. These specimens, described here as *L. emmotti*, are both morphologically and biochemically distinct from *L. punctatovittata*. However, monostylar individuals from central Queensland, which appear to be morphologically indistinguishable from *L. punctatovittata*, are biochemically distinct from the more easterly and southerly populations of this species.

Clearly, *L. punctatovittata* as currently recognised is a composite species. Unfortunately the locality given for the holotype is simply 'Queensland'. Although it is tempting to assume that this specimen was most likely collected from more coastal populations, such an assumption would be unsound because considerable settlement of western Queensland had taken place by the time *L. punctatovittata* (Günther, 1867) was described. The distribution of *L. punctatovittata* and the description of cryptic forms within this species complex warrant further investigation.

As well, even though we have assigned didactyl specimens from NSW/SA to *L. emmotti*, nevertheless the possibility remains that some populations of *L. punctatovittita* are polymorphic for the didacty-monodactyl condition. This possibility should be tested by further allozyme analysis.

The holotype of *L. punctatovittata* (Natural History Museum, London BMNH 1946.8.18.80; Cogger et al, 1983) has a monostylar forelimb (Boulenger, 1887) and is not a specimen of *L. emmotti*. Cogger et al. (1983) listed *Rhodona officeri* McCoy, 1881, as a junior synonym of *L. punctatovittata* and noted that the type material of *officeri* had not been located (see also Coventry, 1970). However, McCoy's description and illustration of the holotype are detailed. The specimen agrees in all characteristics with *L. punctatovittata*, including having a monodactyl forelimb. We therefore concur with the synonymy of Cogger et al., (1983).

This study highlights the power of combining morphological character analysis with an independent genetic technique, such as allozyme electrophoresis, to assess the systematic significance of seemingly trivial morphological variation.

ACKNOWLEDGEMENTS

We thank Steve Wilson for the use of his photograph, Angus Emmott for finding many of the specimens, Robert Raven for drawing Fig. 4 and Neale Hall for typesetting the paper in Ventura. Ross Sadlier (Australian Museum) and Mark Hutchinson (South Australian Museum) gave us access to the collections in their care. Some of the frozen tissue specimens were collected with the assistance of an Australian Research Council grant awarded to M. Adams and P. Baverstock. We also thank Craig Moritz.

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NEW RECORDS OF THE RARE GREEN-THIGHED FROG. *Memoirs of the Queensland Museum 33(1): 348. 1993:-* The Green-thighed Frog (*Litoria brevipalmata*) is a mysterious frog, populations of which apparently suddenly appear and disappear at a locality—sometimes the 'absences' are for many years (Tyler & Davie, 1985). These disappearances, however, do not appear to be part of the phenomenon of the 'disappearing frogs' (sensu Czechura & Ingram, 1991) because the species is still extant.

Until recently, the Green-thighed Frog was known from only three locations in Queensland. McDonald (1974) collected a specimen at Crows Nest National Park (NP 629: 27°15'S, 152°06'E) and another from Ravensbourne National Park (NP 492: 27°21'S, 152°12'E). Four years later, the species was collected near Jimna (26°39'S, 152°27'E) (Czechura, 1978) and in 1983 Chris Corben collected two specimens (Queensland Museum [QM] J42134, 42135) also near Jimna. All these records are from montane country.

Recently the senior author collected two male Green-thighed Frogs alongside Woogaroo Creek near Wacol, Brisbane (27°36'S, 152°54'E). These are the first coastal records for this frog in Queensland and add to the frog fauna of the Brisbane area. These records are reported here. Frog names follow Ingram et al. (1993).

First collection, 21 November 1992

At Woogaroo Creek near Wacol, heavy rain, with lightning, began falling at about 4.30pm and by 5.00pm there were radio reports of local flooding. Rain then reduced to a steady light fall with intermittent heavier showers. Observations began at about 8.00pm at a large L-shaped depression ('Ric's Ditch'), some 40m in length, alongside Woogaroo Creek and some 30m from the main creek-line. From previous experience, this depression became an ephemeral pool after good rain. On the day before, considerable rain had fallen in the afternoon and evening but not enough to produce free-standing water. By contrast, the rainfall of the 21st resulted in 85cm of water at the deepest point of the depression.

Amongst the extremely loud chorus of a large number of frogs, an unfamiliar call was heard. This proved to belong to a male *L. brevipalmata*, which was immediately captured (QM J56813). Several more calling males were observed but not collected and, judging from their calls, about 20 males were present at the site; no females were observed. Typical calling sites were in leaf litter about 0.5-0.9m from the water's edge. No Green-thighed Frogs were found away from the depression.

The following species of frogs were also noted: *Limnodynastes ornatus, L. peronii, Litoria caerulea, L. fallax, L. gracilenta, L. rubella, Adelotus brevis and Mixophyes fasciolatus.* Curiously, although the Cane Toad (*Bufo marinus*) was seen well away from the site on a nearby sealed road, none was heard calling or seen in the depression despite what appeared to be ideal breeding conditions.

The vegetation surrounding Ric's Ditch is open dry sclerophyll forest with a sparse, predominately acacia understorey and a ground cover of exotic herbs and grasses. Closer to the creekline there is a heavy infestation of Chinese Elm (*Celtis sinensis*), Camphor Laurel (*Cinnamomum camphora*), a dense understorey of Bush Lanata (*Lantana camara*) and a variety of native species that form depauperate, dry rainforest.

No frogs were observed at the site on the two following nights (22, 23 November), although calls of *Adelotus brevis* and *Limnodynastes peroni* were heard. Within ten days, there was no follow-up rain and the depression became completely dry — all tadpoles apparently perishing.

From 21 November 1992 to 5 January 1993, some rain fell intermittently but not enough to produce any significant frog activity. However, on some occasions these falls were accompanied by, or quickly succeeded by, strong breezes and it is possible the accompanying noise hid the sounds of calling frogs. From 1 January 1993, rainfall was recorded near Ric's Ditch. On the evening of 4 January 1993, a very brief storm produced 0.6mm and on the next afternoon a more substantial storm resulted in 30mm. At Ric's Ditch, 30mm was insufficient to produce free-standing water. Apart from a brief call from a Naked Treefrog (*Litoria rubella*), the only active caller was the Red-backed Broodfrog (*Pseudophryne coriacea*), with about 30 frogs that called from small, natural tunnels in very porous substrate.

Second collection, 6 January 1993

In the late afternoon, a vigorous electrical storm resulted in a fall of 48.5mm and, by 8.00pm, a loud chorus of frogs came from Rics' Ditch. About a dozen Green-thighed Frogs were calling and another male was collected (QM J57285). The same species of frogs noted on 21 November 1992 were recorded again and Cane Toads were also absent.

The next day was overcast with occasional light rain. Very light rain was falling at about 7.30pm when Ric's Ditch was revisited. There were about twice as many males of Green-thighed Frogs calling compared to the night before and several of the these were much closer to the water, with one about 10 cm from shallow water. As before, no females were observed.

An immediate visit was made to the neighbouring Six Mile Creek some 8km distant and observations were made at several sites. A slightly different frog fauna was recorded. *Litoria nasuta* and *Crinia parinsignifera* were numerous in open grassy areas. In a melaleuca swamp, there were *Limnodynastes terraereginae* and *Litoria dentata*. In the Bracken Fern (*?Pteridium esculentum*) the Dusky Gungan (*Uperoleia fusca*) was recorded. However, despite considerable searching over a wide area, the Green-thighed Frog was not found.

Since 6 January, until now (22 May 1993), the Green-thighed Frog has not been met with at Woogaroo Creek, despite repeated visits.

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EARLY PERMIAN INADUNATE CRINOIDS FROM THAILAND

GARY D. WEBSTER AND PETER A. JELL

Webster, G.D. & Jell, P.A. 1993 06 30: Early Permian inadunate crinoids from Thailand. *Memoirs of the Queensland Museum* **33**(1): 349-359. Brisbane. ISSN 0079-8835.

Eight species of Early Permian inadunate crinoids are described from Ko Muk, Ko Phi Phi, and Ko Yao Noi, islands off southern Thailand. These are the first Palaeozoic crinoids described from Thailand and support an Early Permian age for the Phuket Group and Rat Buri Limestone. New species described are *Kallimorphocrinus thaiensis*, *Apographiocrinus komukensis*, and *Contocrinus andamanensis*; five species are left in open nomenclature. □ *Permian, crinoids, inadunate, Thailand.*

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Permian rocks are widespread in Thailand (Waterhouse & Piyasin, 1970, fig. 1; Lumjuan & Lovacharasupaporu, 1984). Since 1960 systematic studies, including stratigraphic interpretations have concentrated on brachiopods (Yanagida, 1984), fusulinids (Toriyama, 1984; Ingavat, 1985), and bryozoans (Sakagami, 1984). This paper is the first to describe Permian crinoids from Thailand.

LOCATION AND STRATIGRAPHY

Crinoids were derived from five localities on the islands of Ko Muk, Ko Phi Phi, and Ko Yao Noi northwest of Kan Tang in the Andaman Sea off southern Thailand. Maps of the islands showing general position of fossil localities are as follows: 1, upper Phuket Group, SW side of Ko Muk, with stratigraphic sections (Waterhouse, 1982, figs 2b,3,4); 2, upper part of Phuket Group and 3, basal part of Rat Buri Limestone, Ko Phi Phi, indicated on measured section of Tong Lang Bay (Waterhouse, 1982, fig. 2a); 4, Rat Buri Limestone, Ko Muk, U.S. National Museum locality 9271 (Grant, 1976, fig. 7); and 5, Rat Buri Limestone, Ko Yao Noi, (Waterhouse et al., 1981), fig. 4. An unsuccessful attempt was made to locate the calyx reported by Waterhouse (1982, p. 339), from the Phuket Group on Ko Phi Phi for inclusion in this study.

In southern Thailand Phuket Group brachiopods are considered Sakmarian (Waterhouse et al.,1981; Waterhouse,1982). The Rat Buri Lst has been considered Artinskian (Sakagami,1970; Yanagida,1970; Grant,1976), late Early Permian (Yanagida,1984), Kazanian (Waterhouse & Piyasin,1970) or Kungurian (Waterhouse,1981).

The Rat Buri Limestone has been applied somewhat indiscriminately to Permian limestones throughout Thailand (Grant, 1976). Diversity of carbonate microfacies within the Rat Buri Limestone is reflected in the reports of many beds with restricted faunas, i.e., fusulinids with rare or no brachiopods or abundant brachiopods and bryozoans with no fusulinids (Grant, 1976). Fusulinids are virtually unknown in the Rat Buri Limestone in peninsular Thailand (Toriyama, 1984, fig. 1), but in central and northern Thailand fusulinids range from Sakmarian to Dorashamian (Ingavat, 1985). A Sakmarian ammonoid fauna occurs in the basal Rat Buri Limestone in central Thailand (Glenister et al., 1990). Waterhouse (1981) correlated the Rat Buri Limestone of southern Thailand with the Bitauni Beds of Timor. However, the Bitauni Beds are considered Artinskian based on ammonoids (Glenister & Furnish, 1987).

Considerable work remains in determining stratigraphic relationships of the Rat Buri Limestone throughout Thailand. However, sufficient palaeontological information is available to evaluate the age of the unit at most localities. Based on fusulinids and ammonoids the base of the Rat Buri Limestone in central and northern Thailand is Sakmarian or Artinskian. In peninsular Thailand we consider the Rat Buri Limestone to be of Artinskian age based on data of Sakagami (1984) and Yanagida (1984) and correlation of the brachiopod faunas with the Timorese Bitauni fauna (Grant, 1976; Waterhouse, 1981).

Clastic sediments of the Phuket Group have been referred to as cool water deposits equivalent to glaciomarine deposits of Gondwanaland (Waterhouse, 1982 among others). Altermann (1986) considered these deposits to represent deposition on a continental margin lacking sufficient evidence to interpret them as glaciomarine. Brachiopods from a carbonate band within the pebbly

mudstones in the upper part of the Phuket Group were interpreted by Waterhouse (1982) as mostly cool temperate genera. Brachiopods from the Rat Buri Limestone were interpreted (Grant, 1976) as tropical with marine connection to cooler water. Waterhouse (1982) considered the brachiopod faunas of the Rat Buri Limestone to have a stronger cool temperate composition.

FAUNAL SIGNIFICANCE

All crinoids reported are allagecrinid or advanced poteriocrinitid cladids. The allagecrinid *Kallimorphocrinus* occurs in the Carboniferous and Permian in North America, the Carboniferous of Europe and Permian of Timor and Russia (Bassler & Moodey, 1943; Webster, 1973, 1977, 1986, 1988). *K. thaiensis* and *K.*? sp.nov. from the Phuket Group are related to Permian *Kallimorphocrinus* and *Wrightocrinus* from Timor.

The dorsal cup from the Phuket Group, assigned to *Cymbiocrinus* is the second report of the genus from the Permian and outside North America. Cymbiocrinids are considered the ancestral stock of the calceolispongiids, a Tethyan family restricted to the Permian of Australia, Timor and India (Moore & Strimple in Moore & Teichert, 1978). The bulbous basals of *Cymbiocrinus* are considered a continuation of the cymbiocrinid lineage in parallel with the calceolispongiids which had branched off earlier.

The other advanced poteriocrinitids from the Rat Buri Limestone are small specimens, perhaps not fully mature. They belong to genera that are relatively small but typically larger than these specimens. *Apographiocrinus* is known from the Upper Carboniferous and Lower Permian of North America and the Permian of Russia, Timor and Western Australia (Bassler & Moodey, 1943; Webster, 1973, 1977, 1986, 1988). *A. komukensis* is most similar to *A. pumilus* of the Early Permian Callytharra Formation of Western Australia (Webster, 1987) and Permian Basleo Beds of Timor (Wanner, 1916). The partial crown questionably assigned to *Apographiocrinus* has a more elongate cup than is typical in the genus. This may reflect immaturity as height:width ratio of the cup may decrease with growth as in other inadunates (Pabian & Strimple, 1985).

Contocrinus is known only from the Late Carboniferous and Early Permian of North America (Webster, 1973, 1977). The advanced condition of the anal interarea in *Contocrinus andamanensis* sp.nov. suggests a Permian age. The partial crown questionably assigned to the Clathrocrinidae has arm structure similar to the Late Carboniferous *Clathrocrinus* known only from North America (Webster, 1977, 1986). Cup features suggest advanced morphology common in Late Carboniferous or Permian poteriocrinids.

None of the three poteriocrinid genera from the Rat Buri Limestone are restricted to the Permian; they occur in the Late Carboniferous and Permian or Late Carboniferous only. The lack of strong ornament on the cladids may indicate they are farther offshore or deeper water forms (Pabian & Strimple, 1985). Preservation of crowns with proximal columnals attached implies little if any postmortem transport.

Crinoid ossicles are common elements with brachiopods and bryozoans in shallow shelf carbonates and marls in the late Palaeozoic (Lane & Webster, 1980; Pabian et al., 1989). All Thai crinoids discussed were associated with brachiopods and bryozoans. However, crinoids were sparse in residues from the Phuket Group and the Rat Buri Limestone. Some samples were totally lacking in crinoidal debris. This is considered a reflection of some paleoecologic control, perhaps water temperature.

SYSTEMATIC PALAEONTOLOGY

Morphologic terminology follows Moore & Teichert (1978). Specimens are reposited in the: United States Nation Museum (USNM), University of Tasmania (UT) and University of Queensland (UQ).

Class CRINOIDEA Miller 1821
Subclass INADUNATA Wachsmuth & Springer, 1885
Order DISPARIDA Moore & Laudon, 1943
Superfamily ALLAGECRINOIDEA Carpenter & Etheridge, 1881
Family ALLAGECRINIDAE Carpenter & Etheridge, 1881

Kallimorphocrinus Weller, 1930

TYPE SPECIES

K. astrus typicum (=*K. astrus astrus*) Weller,1930 from the Late Carboniferous Perth Limestone, Indiana; by original designation.

Kallimorphocrinus thaiensis sp.nov.
(Fig. 1A–F)

ETYMOLOGY.

From Thailand.

MATERIAL AND LOCALITY

Holotype UQF79668; paratypes UQF79669, 79670, silica replacements of thecae from a Permian unit, probably the Rat Buri Limestone, on Ko Muk.

DIAGNOSIS

Radials gently rounded, tumid. Thecal outline rounded pentalobate in oral view.

DESCRIPTION.

Theca bowl-shaped, higher than wide, greatest width just above midheight, incurved to radial summit, rounded pentalobate in oral view. Dorsal cup tumid, flat-based, bowl-shaped, finely pitted.

BB 2 or 3, sutures obscured by silicification, forming lower 1/3 of cup height in lateral view, RR 5, approximately twice as long as wide, narrower at base than radial summit, convex horizontally and longitudinally, prominently rounded tumid at 3/4 length, subequal in size, becoming wider with increasing facets. Radial summit horizontal, 1-3 facets per radial. Facets with well developed transverse ridge; muscle field in moderately deep depression sloping inward to ambulacral canal. Anal facet small, equidimensional, on left shoulder of C radial. OO 5, well elevated, slightly inset on radial summit, forming a quarter thecal height, dart-shaped, shaft sides vertical, oral surface with two faint ridges parallel to sides, extending nearly to centre of circlet. Posterior oral largest, separating BC and DE orals, probably bearing hydropore or madreporite. Proximal columnal circular transversely, much wider than high.

MEASUREMENTS OF HOLOTYPE (mm)

Thecal height, 3.1; maximum width, 2.6; height BB circlet, 0.9; radial length 1.6, width, 1.4; height OO circlet 0.7; proximal columnal diameter 1.3, height 0.2.

REMARKS.

The description is based on the holotype, a specimen with 9 arm facets, 2 on A and B radials, 1 each on the C and E radials, and 3 on the D radial, and the paratype, a partial theca lacking the basal circlet and adjacent basal ends of the radials. The paratype bears one arm facet on each radial and the A facet appears to have the initial stage of a second facet developing on the right side. Both specimens fit the generic definition as revised by Lane & Sevastopulo, 1982.

Kallimorphorinus thaiensis is distinguished by the rounded protuberance of the radials being greatest at 1/2 thecal height. The Early Carboniferous, *K. astrus* and *K. piasaensis*, also have their greatest protuberance below the radial facet but their protuberance is much sharper making their thecae more pointed pentalobate in lateral and oral views. The only other Permian species, *K. eaglei* (Strimple, 1966), from Oklahoma and Nevada has exceedingly bulbous radials and much lower basals.

An abberant specimen with four orals is assigned to *K. thaiensis*. It has no arm facet on the A radial and the EA and AB orals are fused. There are two arm facets each on the B and D radials, and one each on the C and E radials. The BC oral is not preserved but facets for its articulation are visible on the specimen. The A radial is narrower than the other radials and narrowest at the top where it abuts the abnormal oral. The orals are larger and higher than those of the types.

Silicification has obliterated details of ornament and oral and radial facets. All are judged to be immature as they retain the oral plates.

Kallimorphocrinus? sp.
(Fig. 1G–J)

MATERIAL AND LOCALITY.

UQF79666, 79667, silica replacements of thecae associated with *K. thaiensis* from the Early Permian Rat Buri Limestone, Ko Muk.

DESCRIPTION.

Theca truncate bowl-shaped, higher than wide in immature forms, wider than high in more mature forms, walls gently flared outward nearly to radial summit, widest just below radial summit. Dorsal cup rounded pentalobate in oral view, walls smooth.

BB circlet fused, low, forming lower 1/4 of cup in immature forms, shallowly concave on circular facet for stem attachment, flaring upward from edge of stem facet. RR 5, longer than wide, narrowest at base, flaring gently outward nearly to facet, moderately convex transversely; convexity increasing distal of facet, becoming wider with increasing number of facets. Radial facets with transverse ridges, outer ligament pits and muscle fields on deep pit sloping inward, with one or more facets per radial in adults. Anal notch small, on left shoulder of C radial.

OO 5, forming rounded dome; individually approximately dart-shaped, widest medially; walls straight, vertical; oral surface with shallow central depression bordered by narrow U-shaped rim closed on aboral end.

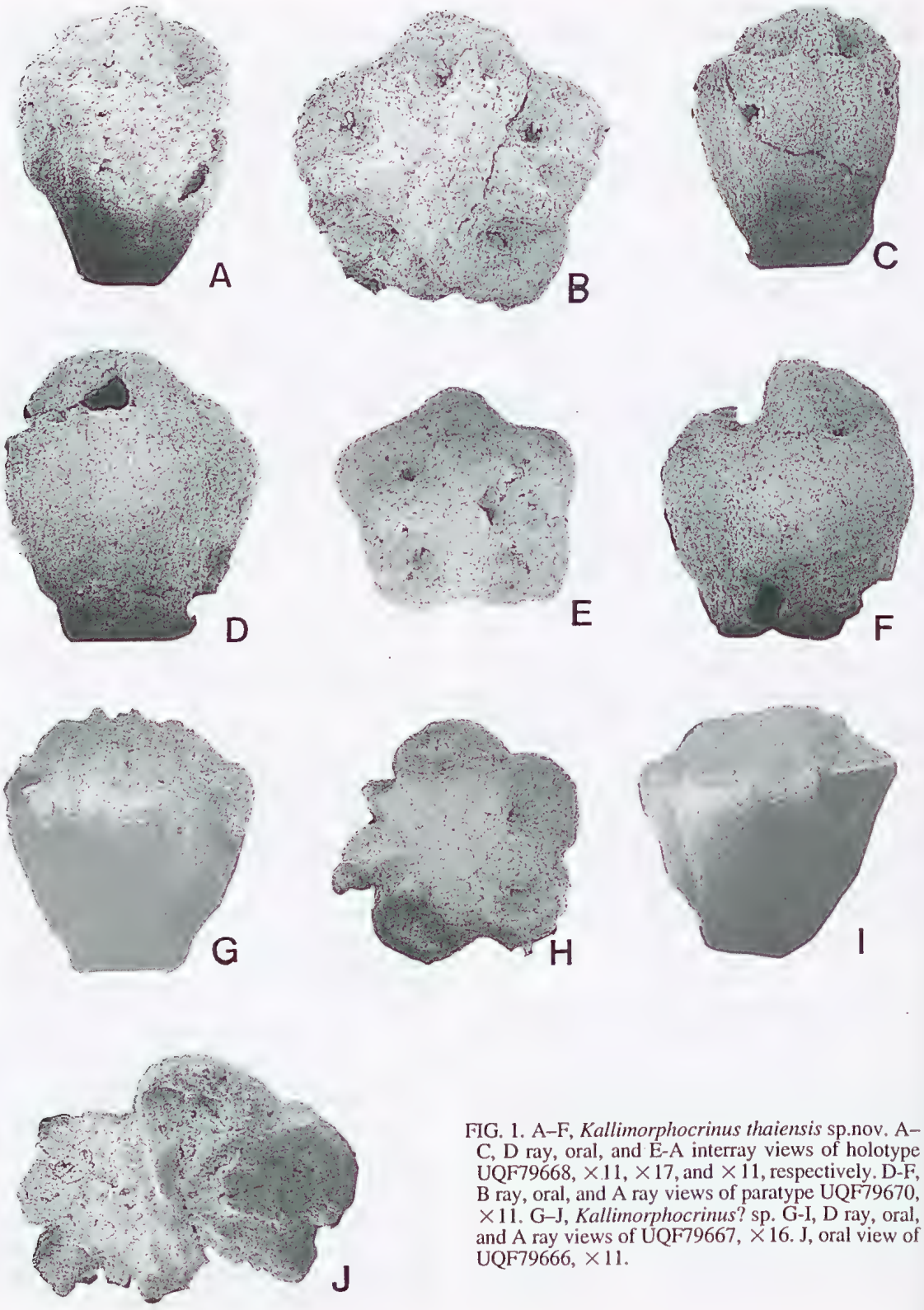

FIG. 1. A–F, *Kallimorphocrinus thaiensis* sp.nov. A–C, D ray, oral, and E-A interray views of holotype UQF79668, ×11, ×17, and ×11, respectively. D-F, B ray, oral, and A ray views of paratype UQF79670, ×11. G–J, *Kallimorphocrinus*? sp. G-I, D ray, oral, and A ray views of UQF79667, ×16. J, oral view of UQF79666, ×11.

MEASUREMENTS (mm)

	U Q F 79666	U Q F 79667
Height of theca	2.0	3.4*
Max. width of theca and cup	2.0	4.5
Height of dorsal cup	1.7	3.3*
Height of RR	1.3 (A)	3.1 (D)
Width of RR	1.0 (A)	1.8 (D)
Height of BB circlet	0.5	—
Height of OO circlet	0.3	0.1
Diameter of the stem facet	0.8	—

* estimated

REMARKS

The description is based on an immature five-armed theca lacking a small part of the outer wall of the C radial and a larger partial theca lacking virtually all the A radial, most of the B radial, and subjacent part of the basal circlet. This second specimen has one arm facet on the E radial, two on the D radial, one, two or three on the C radial, and at least one on the B radial. Silicification has obliterated some details of the oral plates and radial facet.

Doubts about generic assignment stem from two features. The anal notch could be a result of silicification on the smaller specimen and actually be an arm facet on the larger specimen. Secondly the radials closely resemble those of *Wrightocrinus jakovlevi*, to which this species could be related.

Kallimorphocrinus, as redefined by Lane & Sevastopulo, 1982, has up to 14 arms with only one arm in each of the C and E rays, an anal series, and loss of the orals in adults. Moore (1940) proposed *Wrightocrinus* as an allagecrinid with or without an anal series distinguished by the single arm on each of the B and E radials in adults. He designated *Allagecrinus jakovlevi* Wanner, 1929 as type. Wanner (1929) reported 125 specimens of *A. jakovlevi* and analysed 71 specimens as having 1 arm in each of the B and E rays with one exception having 2 arms in the B ray. Marez-Oyens (1940) reported an additional 199 specimens of *A. jakovlevi* with only 12 specimens having 2 (10 specimens), 3 (one specimen), or 4 (one specimen) arm facets on the B radial. It is possible that most of these exceptions are incorrectly identified and are actually kallimorphocrinids or other allagecrinids as they only have one arm facet on the C and E radials with one exception with two on the C radial.

The number of arms in each ray in adult microcrinoids may be generically diagnostic of some allagecrinids (Moore, 1940; Moore & Strimple in Moore & Teichert, 1978). For example, *Wrightocrinus* normally has only one arm in each of the B and E rays, whereas *Kallimorphocrinus* has one arm in each of the C and E rays, and both genera have more than one arm in each of the other rays. The radials of the two specimens assigned to *Kallimorphocrinus*? sp. are very similar in shape to those of *Wrightocrinus jakovlevi* (Wanner, 1929) a Permian form from Timor. If there were no question about the number of facets on the B and C radials in the larger specimen we would assign the specimens unquestioned to either *Wrightocrinus* or *Kallimorphocrinus*.

The only other species, previously assigned to *Wrightocrinus* is *Allagecrinus biplex* Wright, 1932 (designated genotype of *Thaminocrinus* Strimple & Watkins,1969), a Visean form from Scotland with an anal series. Moore (1940) considered the lack of an anal series in the Permian species to be an advanced evolutionary feature for the genus. Neither Wanner (1929) nor Marez-Oyens (1940) recognised specimens of *A. jakovlevi* with less than 9 arms, however, they both recognised specimens of *A. quinquebrachiatus* Wanner, 1929, a form with 5 arms and no anal series and a cup shape, radial form and oral configuration like that of *A. jakovlevi* but approximately one half the size. Strimple (1966) proposed *Metallagecrinus* designating *A. quinquebrachiatus* as type. If *A. quinquebrachiatus* is the immature form of *W. jakovlevi*, as we believe, then *Metallagecrinus* is a junior synonyum of *Wrightocrinus*.

Strimple (1966) assigned an additional 11 species to *Metallagecrinus* because they all lacked an anal series, retained the oral circlet, and had one arm per ray. Strimple & Sevastopulo (1982) reconsidered these assignments and suggested *M. multibrachiatus* (Yakovlev, 1927), *M. dux* (Wanner, 1930) and *M. inflatus* (Wanner, 1929) should be excluded because they differ in several respects from the type. We agree with this assessment and would transfer all other species [*M. acutus* (Wanner, 1929), *M. excavatus* (Wanner, 1929), *M. indoaustralicus* (Wanner, 1916), *M. quinquelobus* (Wanner, 1929), *M. procerus* (Wanner, 1929), *M. ornatus* (Wanner, 1929), *M. uralensis* (Yakovlev, 1927) and *M. uralensis nodocarinatus* (Yakovlev, 1927) as well as *M. palermoensis* Strimple & Sevastopulo, 1982 to *Litocrinus* Lane & Sevastopulo, 1982.

Order CLADIDA Moore & Landon, 1943
Suborder POTERIOCRININA Jaekel, 1918
Superfamily SCYTALOCRINOIDEA
Moore & Laudon, 1943

Family and Genus uncertain

MATERIAL

One partly silicified dorsal cup, UQF79665, from acid residue of loose boulder of Rat Buri Limestone from the southeast part of small bay; Ban Hat Yao, on the northern end of Ko Yao Noi, southern Thailand.

REMARKS

This cup is 5.8mm wide, 3.4mm high, cone-shaped, with truncated base, steeply outflared plenary radial facets, with a single small anal in a notch shared by the C and D radials. Infrabasals small, slightly upflared. Ornament destroyed by silicification if present; stem facet round. Anal sac and arms unknown.

Advanced features present on the cup are the plenary facets and anal plate nearly out of the cup. A primitive feature retained is the conical shape. The specimen is questionably assigned to the scytalocrinoids because of its shape, radial facets, and number and position of the anal.

The specimen is not well enough preserved to be designated a type or effectively illustrated. It is mentioned because it adds to the generic diversity in the Permian of Thailand.

Superfamily DECADOCRINOIDEA Bather, 1890
Family CLATHROCRINIDAE Strimple & Moore, 1971

Clathrocrinid gen. et sp.nov.
(Fig. 2 O,P)

MATERIAL AND LOCALITY

One crown, USNM450329, from acid residue of the Rat Buri Limestone, locality USNM9271, northwest side of Ko Muk, NW of Kan Tang (Grant, 1976).

DESCRIPTION

Crown small, elongate, subcylindrical, with arm girdle at top of primibrachials, 10 arms slender with offset brachials in zig-zag pattern. Cup crushed, medium bowl; walls outflaring, gently convex; base invaginated; sutures flush; radial notches obvious; ornament lacking. IBB not visible in lateral view. BB 5, slightly longer than wide, gently convex transversely, strongly convex proximally, gently convex distally, proximal end forming base of cup. RR 5, wider than long, gently convex transversely and longitudinally; facet angustary, lacking prong-like internal extensions on lateral ends of upper surface; small gape with primibrachials at facet. Single anal relatively large, longer than wide, with proximal third below radial summit, sitting on top of truncated laterally symmetrical CD basal, with distal two-thirds incurved above radial summit, adjoined distally by two tube plates. IBrr one per ray, axillary, longer than wide, widest at base, laterally constricted in central three-fourths, strongly convex transversely, gently concave longitudinally, bearing prominent slightly upward directed spine at distal end. IIBrr elongate, cuneate, twice as long as wide proximally, three times longer than wide distally, widest on distal end, strongly convex transversely, longitudinally straight becoming concave distally, bearing prominent slightly upward directed spine on distal end. Pinnules large, could be considered ramules, elongate, strongly convex transversely, alternate on sides of arm, one per brachial on distal end of brachial.

MEASUREMENTS (mm)

Crown length 31.6 (incomplete), width 10.6; cup height 5.8, width 4.2 (estimated); BC basal length 3.6, width 3.5; E radial length 4.2, width 5.8; anal length 3.8, width 3.2; IBr1 length 4.1, width 3.8; IIBr1 length 5.8, width 2.8; IIBr5 length 4.6, width 1.7.

REMARKS

No name is given to this distinctive specimen because the cup is crushed. Infrabasals are not preserved; the BD, CD and DE basals and C, D and E radials are preserved.

Classification is based on arm structure. The angustary radial facets, elongate brachials, pinnules that are essentially ramules, zig-zag pattern of the brachials, and spine on the distal end of the brachials all have affinity with the Clathrocrinidae. Unlike *Clathrocrinus* only one anal occurs within the radial summit, indicating an advanced condition, and the zig-zag pattern of the brachials is not as widely spreading. We consider this specimen to have evolved from a clathrocrinid ancestor in Early Permian times. Range of the family is extended into the Permian and its distribution, previously confined to North America, is extended to Southeast Asia.

Superfamily ERISOCRINOIDEA Wachsmuth & Springer, 1886
Family GRAPHIOCRINIDAE Wachsmuth & Springer, 1886

Contocrinus Knapp, 1969

TYPE SPECIES
Graphiocrinus stantonensis Strimple, 1939 from the Upper Carboniferous Wann Formation, Oklahoma, by original designation.

Contocrinus andamanensis sp.nov.
(Fig. 2E–H)

ETYMOLOGY
For the Andaman Sea.

MATERIAL
Holotype USNM450326; paratype USNM450325, Rat Buri Limestone, locality USNM9271, NW side of Ko Muk, Thailand.

DIAGNOSIS
Small, with a shallow arm girdle, large elongate posterior basal, and anal distally adjoined by two tube plates.

DESCRIPTION
Crown elongate, slender, with slight arm girdle at base of secundibrachials, 10(?) arms. Cup medium bowl-shaped, widest slightly below radial summit, with moderate basal invagination; sutures between basals slightly impressed, sutures between radials deeply impressed; apical pits at top of basals and base of radials; granular to vermiform ornamentation. IBB 5, small, slender, strongly tapering, downflaring, not visible in lateral view, covered by proximal columnal. BB 5, outflaring, strongly convex longitudinally and transversely, slightly wider than long, proximally forming base of cup; posterior basal larger, more elongate. RR 5, slightly outflaring, wider than long, strongly tumid. Radial facets plenary, sloping outward, with moderate gape; outer ligament area wide, with pit; transverse ridge full width of facet. Anal slightly longer than wide, proximally adjoining truncated transversely symmetrial CD basal, distal end projecting slightly above radial summit, followed by two tube plates. IBrr one per ray, axillary, medially constricted, strongly convex transversely, gently concave longitudinally, slightly wider proximally than distally. IIBrr slightly longer than wide, slightly cuneate, strongly convex transversely, weakly convex longitudinally; sutures slightly impressed. Proximal columnals heteromorphic, transversely round, latus convex, symplexy articulation; lumen not preserved.

MEASUREMENTS (mm).

	U S N M 450325	U S N M 450326
Crown length (incomplete)	14.0	15.0
Cup height	2.0	3.4
Cup width (through A-CD)	5.9	7.3
Diameter IBB circlet		0.9
AB basal length	1.8	2.4
AB basal width	1.9	2.8
A radial length	1.7	2.4
A radial width	2.8	3.2
IBR1 length	2.9	4.5
IBR2 width	2.8	3.7
IIBR1 length	1.9	2.3
IIBR1 width	1.7	2.2
IIBR5 length	1.2	1.4
IIBR5 width	1.0	1.9
Anal length	1.8	1.6
Anal width	1.4	1.5
Diameter proximal columnal	1.5	1.3

REMARKS
There are probably 10 arms. The D and E rays are not preserved on the paratype and the A, B and E rays are not preserved on the holotype. All preserved rays bear 2 arms. Pinnules are not preserved on either specimen but articular facets for the pinnules are poorly preserved on the distal outer corner of some of the distal secundibrachials. Noditaxis patterns are not well developed on the proximal pluricolumnal segment, but variable thicknesses of the 6 columnals suggest a simple heteromorphic Type 1 pattern of Webster (1974). Ornamentation is more finely granular on the holotype than the paratype.

These specimens are transitional between the graphiocrinids and apographiocrinids. The arm girdle and two tube plates adjoining the anal plate relate the specimens to the apographiocrinids. However, plenary radial facets and lack of prong-like extensions on the radials between the facets show affinity to the graphiocrinids. We consider the plenary radial facets to be of greater importance in classification than the number of tube plates adjoining the anal plate.

Contocrinus andamanensis has less tumid cup plates and a longer posterior basal than the most similar *C. scopulus* (Lane & Webster, 1966). Both

species are smaller than Pennsylvanian species; because both are based on few specimens, it is not known if they are mature or not.

This is the first report of *Contocrinus* outside North America, although graphiocrinids, i.e. *Permiocrinus* Wanner,1949 is known from Timor. Most Timor species initially assigned or transferred to *Graphiocrinus* by Wanner, 1949, have been assigned to other families of advanced poteriocrinids (Webster, 1987, among others).

Superfamily APOGRAPHIOCRINOIDEA Moore & Laudon, 1943
Family APOGRAPHIOCRINIDAE Moore & Laudon, 1943

Apographiocrinus Moore & Plummer, 1940

TYPE SPECIES

A. typicalis Moore & Plummer, 1940 from the Pennsylvanian Plattsburg Limestone, Kansas, U.S.A., by original designation.

Apographiocrinus komukensis sp.nov.
(Fig. 2A–D)

ETYMOLOGY

From the island of Ko Muk.

MATERIAL

Holotype USNM450328 and paratype USNM450327 from acid residues of Rat Buri Lst at locality USNM9271, NW side of Ko Muk.

DIAGNOSIS

High cup, with less tumid plates, ornament variable, finely granular to vermiform.

DESCRIPTION

Cup medium bowl-shaped, nearly twice as wide as high; walls gently convex, outflared; base with moderately deep invagination; sutures weakly impressed; apical pits shallow; ornament very fine and granular. IBB 5, small, dart-shaped, downflaring, not visible in lateral view. BB 5, slightly wider than long, gently convex transversely and longitudinally, proximal end forms base of cup and edge of basal invagination. RR 5, wider than long, gently convex longitudinally, strongly convex transversely; facets angustary, sloping outward; internally extending prong-like ridges separating facets; well developed radial notches in lateral view. Anal slightly longer than wide, proximal end adjoins truncated laterally symmetrical CD-basal, distal third extends above radial summit, facets for two adjoining tube plates distally. IBrr one per ray, slightly longer than wide, constricted medially, transversely convex, longitudinally concave; axillary, isotomous branching. Stem impression round.

MEASUREMENTS (mm)

	USNM 450328	USNM 450327
Crown height	4.2	3.0*
Cup width	7.6	6.0
Diameter IBB circlet	2.0	1.5
AB basal length	2.5	2.0
AB basal width	2.9	2.4
A radial length	2.4	2.0
A radial width	4.0	3.4
Anal length	2.1	—
Anal width	1.6	—
IBR1 length	—	2.9*
IBR1 width	—	2.7

*estimated

REMARKS

The paratype has more tumid cup plates, some vermiform ornamentation, more impressed sutures, and a lower, more outflaring bowl configuration than the holotype. Although possibly distinct species we consider them one on available material. Angustary radial facets, prong-like projections between radial facets, and facets for two tube plates distal to the anal relate these forms to *Apographiocrinus*.

Three species of *Apographiocrinus*, *A. pumilus*, *A. quinquelobus*, and *A. rugosus*, although initially assigned to other genera, were reported from Permian strata of Timor by Wanner, 1916. All three species have much coarser ornament, ornament of a different type, or much more tumid basals and radials than *A. komukensis*. Late Carboniferous species of *Apographiocrinus* known from North America have less tumid cup plates, are much larger, and have more outflared cup walls than *A. komukensis*.

Apographiocrinus? sp.nov.
(Fig. 2L–N)

MATERIAL AND LOCALITY

One partial crown, UTGD124566 from the basal part of the Rat Buri Limestone from Ko Phi Phi, an island northwest of Kan Tang, recovered by Clive Burrett. Sample No KP(B).

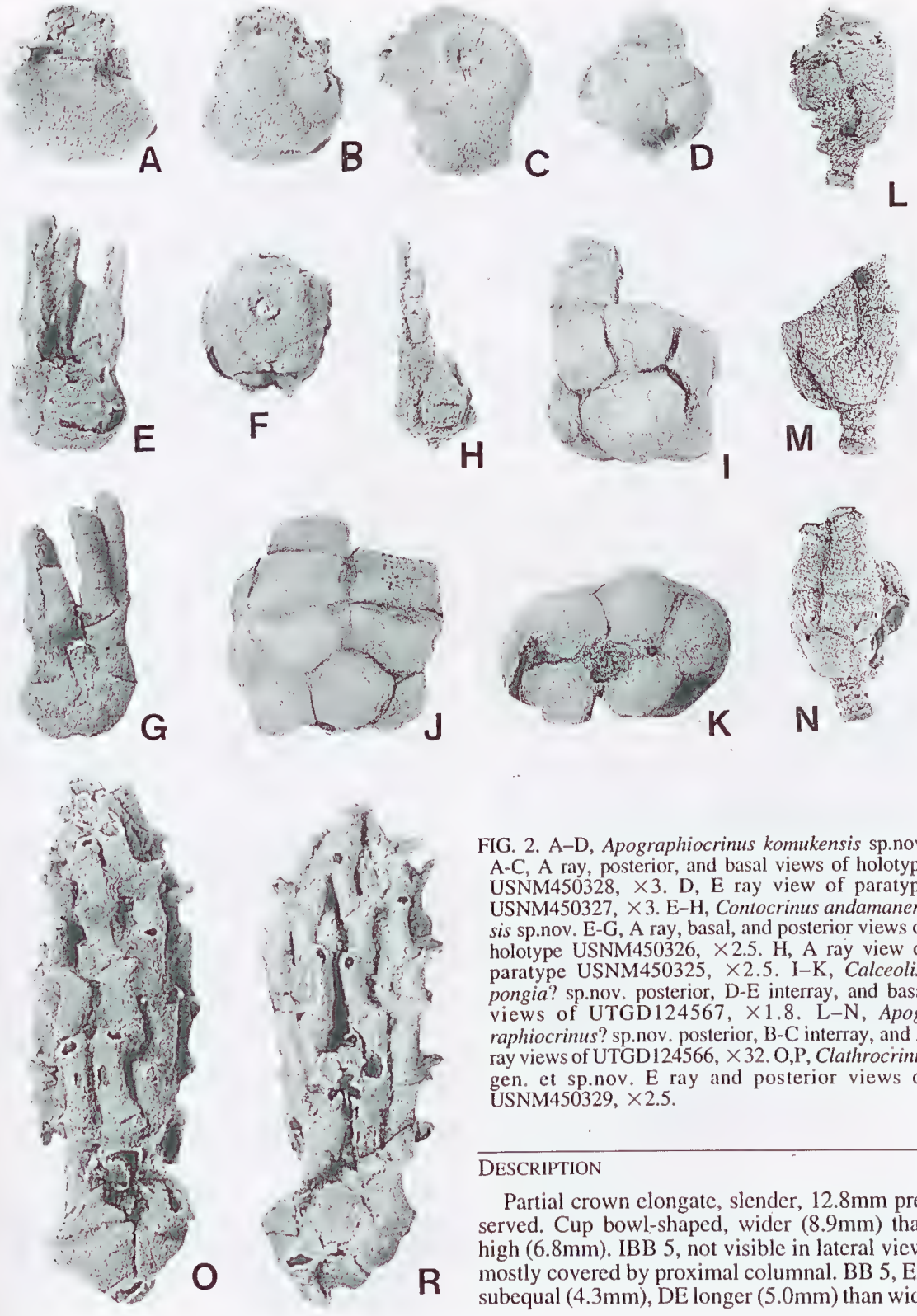

FIG. 2. A–D, *Apographiocrinus komukensis* sp.nov. A-C, A ray, posterior, and basal views of holotype USNM450328, ×3. D, E ray view of paratype USNM450327, ×3. E–H, *Contocrinus andamanensis* sp.nov. E-G, A ray, basal, and posterior views of holotype USNM450326, ×2.5. H, A ray view of paratype USNM450325, ×2.5. I–K, *Calceolispongia*? sp.nov. posterior, D-E interray, and basal views of UTGD124567, ×1.8. L–N, *Apographiocrinus*? sp.nov. posterior, B-C interray, and A ray views of UTGD124566, ×32. O,P, *Clathrocrinid* gen. et sp.nov. E ray and posterior views of USNM450329, ×2.5.

DESCRIPTION

Partial crown elongate, slender, 12.8mm preserved. Cup bowl-shaped, wider (8.9mm) than high (6.8mm). IBB 5, not visible in lateral view, mostly covered by proximal columnal. BB 5, EA subequal (4.3mm), DE longer (5.0mm) than wide

(4.8mm), convex proximally forming basal plane, gently convex and subvertical distally. Posterior basal heptagonal, truncated distally for reception of anal. RR 5, A radial wider (4.8mm) than long (3.5mm), moderately convex transversely, gently convex longitudinally, subvertical to slightly incurved distally, lateral sutures impressed. Radial facets peneplenary, sloping gently outward, low lateral prongs extending internally as lateral ridges with adjoining radials. Single anal longer (2.9mm) than wide (2.1mm), gently convex transversely and longitudinally, proximal 3/4 below radial summit, adjoins 2 tube plates distally.

IBrr one per ray, axillary, longer (6.5mm) than wide (4.5mm) widest at base, longitudinally convexo-concave, transversely convex, constricted below distal facets, unequal in length, ?A ray IBr longest. Proximal columnals heteromorphic, transversely rounded, latus gently convex, lumen ?pentalobate.

REMARKS

The specimen is silicified and slightly distorted basally. Parts of B radial and AB through CD basals not preserved. Only A and E IBr complete, C & E IBr partly preserved. The infrabasal circlet is not visible but internal walls of etched basals show two facets for attachment to infrabasals. There were probably 5 small infrabasals down-flared or subhorizontal.

The arms branch isotomously on the E and A primibrachs, suggesting 10 arms if the same branching pattern occurred in all rays.

The specimen is referred to the Apographiocrinidae because it has peneplenary radial facets, lateral prongs on the radial facets, and 2 tube plates distal to the single anal. The cup is more elongate than in the rest of the family, indicating a less advanced form than might be expected in a Permian member. Constriction in the distal part of the primibrachs suggests development of an arm girdle. It is left in open nomenclature in hope of future recovery of additional specimens.

Cymbiocrinus? sp.nov.
(Fig. 2I–K)

MATERIAL AND LOCALITY

Partial crown, UTGD124567, found by Clive Burrett in the upper Phuket Group on Ko Phi Phi. It occurs in a unit with Early Permian brachiopods considered to indicate a temperate climate (Waterhouse, 1982).

DESCRIPTION

Partial crown crushed subparallel to anterior-posterior plane of symmetry. Cup moderate bowl-shaped, with shallow to moderate basal invagination; plates bulbous, not ornamented. IBB not preserved. BB 5, strongly convex in all directions, subequal length (8.4mm) and width (8.1mm), forming basal plane, hexagonal except heptagonal posterior basal truncated for anal plate. RR 5, half again wider (10mm) than long (6.3mm), convex longitudinally and transversely. Radial facets plenary.

Single large anal, essentially below radial summit, gently convex longitudinally and transversely, longer (4.7mm) than wide (4.6mm). IBrr 2 in B ray, wider (9.7mm) than long (5.2mm) gently convex longitudinally and transversely. IBr2 axillary. C ray IBr larger, 10.2mm wide, 5.8mm long, non-axillary. Additional brachials and stem not preserved.

REMARKS

Specimen replaced by hydrous iron oxides, B radial lost, some loss by solution of plates adjacent to B radial. Radial facets well developed and sloping inward but solution has destroyed details of exposed surfaces. Infrabasals lost, small, probably 5 and down flared or subhorizontal, mostly covered by proximal columnals. Pluricolumnal segments in the matrix block are transversely rounded but not attached to the cup. It is not certain that they were part of the original animal but it seems likely.

The bulbous basals and large radianal suggest relationship with the calceolispongiids. However, branching on the second primibrach is unknown in the calceolispongiids but is typical of *Cymbiocrinus* which has a single anal. We consider the calceolispongiids to have evolved from the Cymbiocrinids adapting to cooler water clastic dominated environments of the Permian of Australia. The specimen is left in open nomenclature in hope of a future discovery of a better specimen to serve as holotype.

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LATE TRIASSIC HOMOPTEROUS NYMPH FROM DINMORE, IPSWICH BASIN. *Memoirs of the Queensland Museum 33(1): 360. 1993*:- This well-preserved homopterous nymph was collected by Mr Robert Knezour from plant fossil-rich mudstone underneath powerlines in a quarry (Queensland Museum [QM] L471) at the end of Roberts St, Dinmore in the Ipswich Basin (27°31'S, 152°51'E). The sediments belong to the Blackstone Formation of the Ipswich Coal Measures. Palynological data suggest a Late Triassic (Carnian) age (deJersey,1970). Details of stratigraphy and age were given by Rozefelds & Sobbe (1987) who noted other insects (Blattodea, Hemiptera and Coleoptera) in association with a typical *Dicroidium* macroflora.

Order HEMIPTERA
Suborder HOMOPTERA
Superfamily UNCERTAIN

The head with the rostrum arising from the frons near the rear of the head suggests an homopterous form but its relationships are uncertain because comparable nymphs are extremely rare in the fossil record. Of the several homopterous nymphs known (Riek,1974 and references therein) none are similar to the new form being mainly Sternorrhyncha whereas this fossil is more like Auchenorrhyncha nymphs (Carpenter, [1992] did not report any nymphs in families referable to the Auchenorrhyncha). Because several critical features are unclear on the fossil, comparison with nymphs of Recent forms can only be superficial and therefore inconclusive. However, it does suggest similarity to Fulgoroidea. The excessively long rostrum, patches of sensory abdominal tubercles, and long coxae based well away from the midline are known in modern Fulgoridae. However, unlike the fossil described here, coxae of the third fulgorid leg are fixed in the sternite and the free part of the leg begins at the tibia. Familial assignment must remain open.

Knezouria gen.nov.

Type species. Knezouria unicus sp.nov.

Remarks. Although it is possible that this nymph belongs to a named fossil species, there is no way of determining its morphogenic development and no way of relating it to an adult. Therefore, a separate binomial name is justified for a fossil that cannot be assigned to an existing taxon and that is likely to be referred to often.

Knezouria unicus sp. nov. (Fig.1)

Etymology. Latin *unicus*, sole, one only.

Material. Holotype QMF18850a,b (part & counterpart), ventral surface only.

Description. Nymph with rudimentary wings (most obvious posterolaterally on thorax); 13mm long; 7mm wide, abdomen half length of animal. Frons large, diamond-shaped, with subtle transverse and longitudinal ridges meeting at midpoint; rostrum very slender, extending beyond the posterior margin of the abdomen (preserved as an indistict ridge curving off the midline along the thorax then crossing the midline near abdominal midlength); posterior of head indistinct.

Legs with long, stout, oblique coxae, based away from midline and running to midline; femora strong, similar, running obliquely to margin; tibia long, slender, may have fine spines on inner edge; tarsi 0.3 length of tibia, gently curved; pretarsus with two claws.

Fig.1. *Knezouria unicus* gen. et sp. nov. holotype, part and counterpart of ventral surface, ×4.

Abdomen inverted beehive shape, 8 segments clearly evident, with distinct, narrow, median longitudinal ridge, with paired areas of small tubercles on each segment (each one associated with a sensory hair, by analogy with modern Homoptera). Terminal (8th) segment with anal and genital structures in median line well forward of margin, in form of two pairs of lobes directed posteriorly, each pair forming an indistinct U-shaped structure.

Acknowledgements

I am grateful to Mr Robert Knezour for donating the specimen and allowing me to describe it.

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SURVEY OF THE VERTEBRATE FAUNA OF THE DOTSWOOD AREA, NORTH QUEENSLAND

STEVE WILLIAMS, RICHARD PEARSON & SCOTT BURNETT

Williams, S., Pearson, R. & Burnett, S. 1993 06 30: Survey of the vertebrate fauna of the Dotswood area, north Queensland. *Memoirs of the Queensland Museum* **33**(1): 361-378. Brisbane. ISSN 0079-8835.

The results of a survey of mammals, birds, reptiles, amphibians and fish of the Dotswood area west of Townsville are presented. Habitats included in the survey were woodland, open forest, tall open forest, closed forest (rainforest), riparian forest and rocky outcrops. A total of 297 species of vertebrates were observed using a variety of survey techniques including live trapping, pit trapping, observational transects, mist netting and spotlighting. Exact locations of observations and indices of relative abundance of each species are included.
☐ *Survey, vertebrate, mountain, Dotswood, north Queensland, Australia.*

Steve Williams, Richard Pearson & Scott Burnett, Australian Centre for Tropical Freshwater Research, James Cook University of North Queensland, Queensland 4811, Australia;
15 November, 1993.

Fauna surveys, although mostly descriptive, are a basic necessity in the understanding of the ecology of any area. This paper describes a broad survey of the vertebrates in a variety of habitats west of Townsville, undertaken to provide baseline information prior to the proposed development of military training facilities. Despite its proximity to and accessibility from Townsville, the survey area, which includes Dotswood Station, Star Station, High Range Training Area and sections of the Bluewater Range, had never been the subject of any intense biological studies. Consequently, very little published biological information exists for the area. Not only is information on the area poorly represented in the literature, but the wet-dry tropical environment of north Queensland which typifies much of the Dotswood and High Range areas is very poorly understood. This reflects the concentration of Australian zoological and ecological research effort in southern regions and the tropical coastal zone in the past.

The study area is located within the Shire of Dalrymple to the south-west of Townsville (Fig. 1), with the north-eastern and eastern boundaries following the escarpments of the Paluma and Hervey's Ranges. The western boundary is to the west of the Star River and the southern boundary follows the boundary between Dotswood Station and Fanning River Station (Fig. 2).

The total study area of about 2320km^2 comprises the following land tenures:

High Range Training Area (HRTA) 48,669ha
Dotswood Pastoral Lease (No. 44/3176). 155,000ha
Special Lease RAAF training area (N 44/45266) 27,300ha
Occupational License (No. 510) 907ha
Total study area approximately 232,000ha

The landscape descends from the escarpments and hills of Paluma and Hervey's Ranges (altitude c.800m) in the north and east to a complex of dissected plateaux and tablelands with steep slopes to the south, through to areas of low relief (altitude c.250m) in the south-west. The study area is drained by the Star River, Keelbottom Creek, Fanning River and the Reid River. Drainage direction is generally to the south, with all drainage systems except the Reid River draining into the Burdekin River. The Reid River flows into the Haughton River.

The emphasis of the study was on recording the diversity of the vertebrate fauna in each of the major habitat types of the study area, with some regard to relative abundances. Sampling methods were therefore designed to record as many species of mammals, birds, reptiles, amphibians and fish as was possible. Additionally, literature on the study area was reviewed and a reasonably comprehensive species list of the area was compiled.

Additional sources of information included rare and threatened species lists from Queensland National Parks and Wildlife Service (QNPWS); endangered species list from ANZECC (Anon, 1991); assessments of status and lists of rare, endangered, vulnerable and poorly known vertebrates of Queensland, and location records of mammal, bird, reptiles and frogs from the Queensland Museum database (Ingram & Raven,

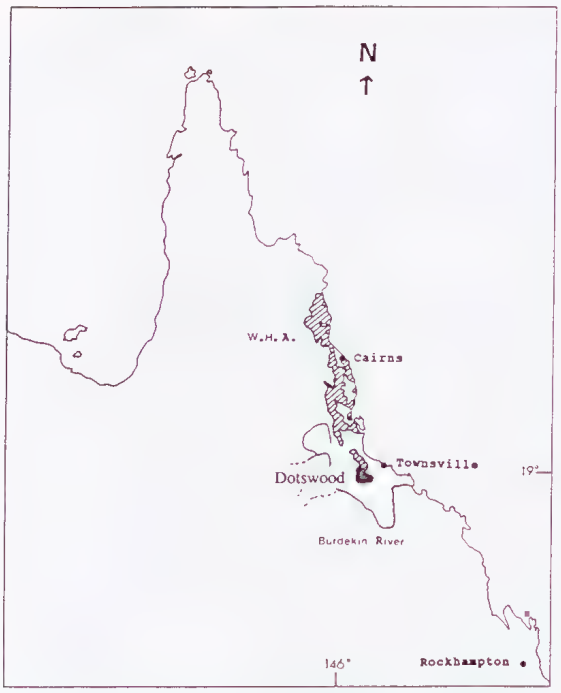

FIG 1. Map of north Queensland showing location of study area.

1991), the most up-to-date assessment of the status of vertebrates in Queensland; species records from the Wildlife Preservation Society of Queensland; Williams et. al., (1993); Ben Lomond . (Hollingsworth, 1980); Brouwer & Garnett's (1990) annotated list of threatened birds of Australia; and a variety of personal communications with staff at James Cook University and the QNPWS.

LITERATURE REVIEW

BIRDS

Most bird records from the region are from the coastal plains and ranges. Lavery & Johnson (1968) provided a list of observations from the Townsville area, from Mt Spec in the north to 'St Helliors' near Cape Cleveland in the south. This study identified 229 species from the area. Blakers et. al. (1984), which provided Australia-wide maps for all the Australian birds mapped in 1°×1° squares (19°S 146°E), recorded 256 spp. from the region encompassing the study area. Nix & Switzer (1991) gave locality and expected ranges of all vertebrates considered to be endemic to the wet tropical rainforest. Steve Garnett (pers. comm.) listed 365 species from the Townsville area and Hollingsworth (1980) listed 64 bird species at the Ben Lomond mine on Dotswood. Queensland Museum specimen records are scanty, including only three species from the Dotswood area.

Due to the relative ease of observation and identification of birds, they feature strongly in the lists of amateur wildlife groups, such as, the Townsville Bird Banding Group, which has undertaken a long term study in tall open forest west of Paluma, and the Wildlife Preservation Society of Queensland, which provides bird lists in excursion reports from the Townsville area, including Bluewater and Hervey's Ranges and Fanning River. In addition, QNPWS provide bird lists for national parks of the area including Mt Spec and the Townsville Town Common. Where relevant, species recorded by these sources have been included in this report.

Ecological studies in the area are much scarcer than simple records of occurrence. Apparently no studies have been conducted within the study area itself or within equivalent open forest in the region. Keast et. al. (1985), however, bring together information on eucalypt forest birds, some of which may be applicable to this area (e.g. Keast, 1985; Recher, 1985).

Rainforest birds have received more attention in north Queensland. Kikkawa (1982) examined the community structure of rainforest birds in relation to rainforest physiognomy and Crome (1978) examined the feeding ecology of birds in lowland rainforest. Although these studies were conducted at lower altitudes than the study area their results should be applicable to rainforest on the Bluewater Range. However, while some studies have been conducted in comparable areas and may be applicable to the study area, information on habitat utilisation, particularly the role of wet refugial areas (i.e. riverine and vine thicket habitats, and responses to disturbance) is scanty. Stocker & Irvine (1983) and Crome & Moore (1990) have discussed the ecological role of the Southern Cassowary in dispersal of rainforest seeds.

MAMMALS

Winter et. al. (1984) provided a list of 16 rainforest mammal species either recorded or expected from the Bluewater region which is partly contained within the RAAF training area. Lavery & Johnson (1968) gave a list of 71 mammals from the coastal plains and ranges of the Townsville area. No equivalent published lists are available from the drier habitats that typify most of the study area, although Hollingsworth (1980) listed

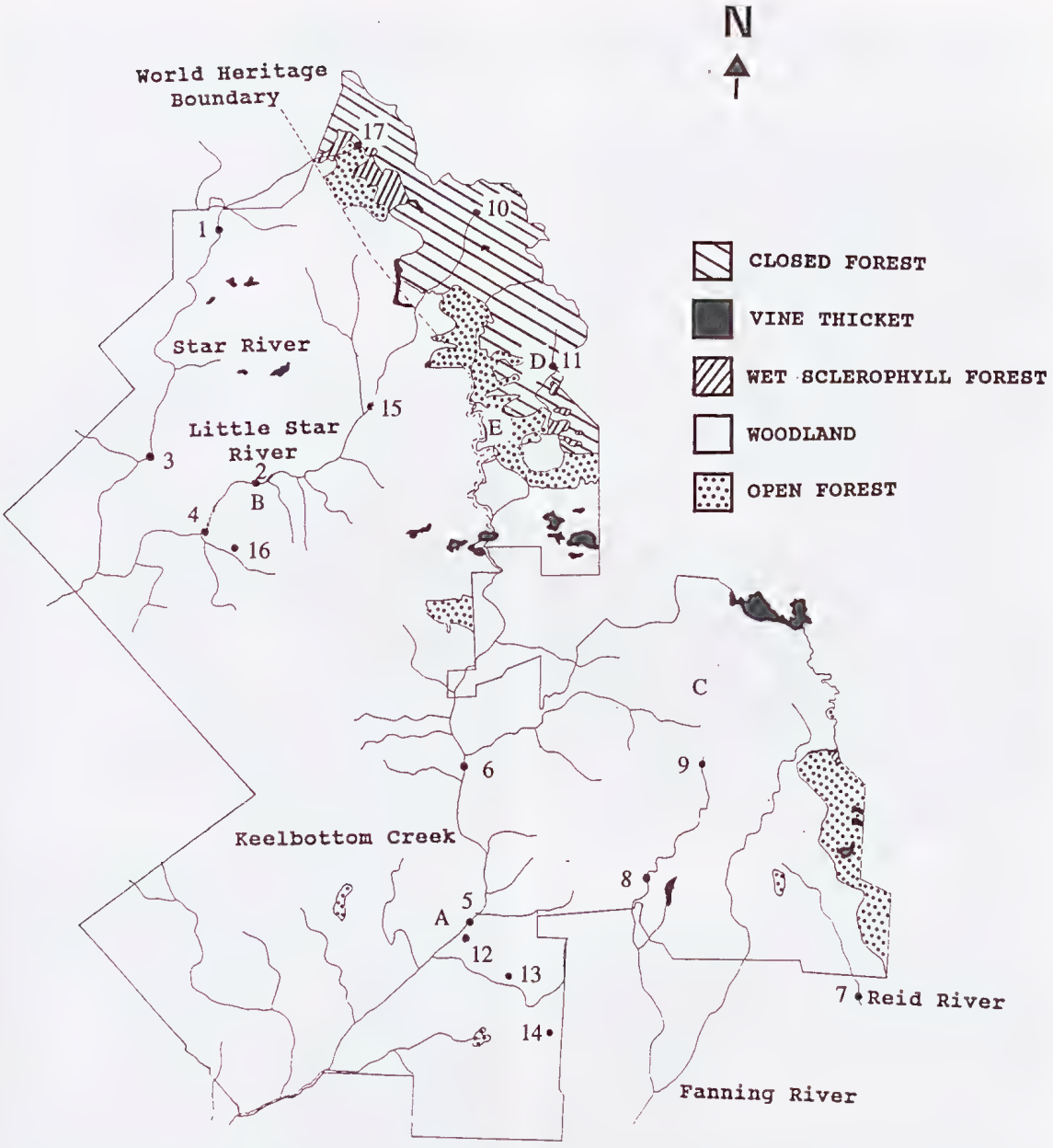

FIG 2. Map of the study area showing site locations and major fauna habitat types and streams (riparian habitat). Major vegetation boundaries after Power & Jackes (1992).

13 mammal species, five of which were introduced, at the Ben Lomond mine site on Dotswood. A QNPWS survey of the Dalrymple Shire covers an area of comparable habitats to the west of the study area, but the results of this survey were not available.

Queensland Museum records provide a list of nine species from Hervey's Range and areas on Dotswood Station while QNPWS provide lists for Mt Spec National Park and Townsville Town Common Environmental Park, which may be applicable to wetter parts of the Dotswood area. At Mt Spec, near Paluma, Williams (1990) examined the relationships between mammal commu-

nities and vegetation in wet forests similar to those in the study area at Bluewater State Forest.

Reptiles

Like mammals, reptiles are mostly cryptic and there is considerable confusion surrounding the taxonomy of many groups. Therefore it is not surprising that, until recently, very little had been published on the distribution and population and community ecology in this group (Strahan, 1985). However, Greer (1989) provided summaries of information on species biology for the lizards.

Queensland Museum records list 27 species of reptiles from the Bluewater/Hervey's Range/Dotswood area and Hollingsworth (1980) listed 23 species at Ben Lomond mine on Dotswood. Both these numbers are probably poor reflections of the true reptile diversity of the area as gleaned from distribution maps (Cogger, 1992; Wilson & Knowles, 1988).

The recent upsurge in interest in the wet tropics has led to increased collecting activity in the area. As a result, the distribution and status of rainforest species is generally better understood than for the species of the drier forest and woodland to the west (e.g. Nix and Switzer 1991). However, for the vast majority of reptiles from this area, and indeed from most of Australia, very little is known of community ecology or of specific habitat requirements (e.g. Wilson & Knowles 1988). The responses of species and communities to natural and human disturbances is unknown.

Amphibians

A considerable increase in interest in frog ecology and taxonomy has happened in the past 20 years (McDonald, 1992; Covacevich & McDonald, 1991; Ingram & Raven, 1991). This increase is reflected in an increase in the number of taxonomic studies (e.g. Czechura et. al., 1987; Liem 1974; Zweifel 1985) and, coupled with recent interest in the wet tropics, has lead to a reasonable understanding of rainforest frog distribution patterns. McDonald (1992) provided a list of 23 rainforest species, 21 of which were endemic to tropical rainforest in north Queensland. Of this list, five, all with conservation prognoses of very good or excellent, are recorded from the Bluewater Range. A further five species are recorded on Queensland Museum lists from the drier areas of the study area and six species are listed from the Ben Lomond mine site on Dotswood Station (Hollingsworth, 1980).

Tyler (1979) described our knowledge of Australian frogs as abysmal and, although they have received much more attention since that time, our understanding of population and community ecology is still at a basic level, especially in the wet/dry tropics. He listed potential impacts of humans on frogs including deforestation, land drainage, introduction of predators (including aquatic predators), and siltation of water bodies. Some species have benefited through human activities including provision of water bodies in dry areas. Habitat utilisation, including, for example, the importance of wet refugial areas, is not known.

Fish

Published material on the aquatic biota of the region is scarce. Pearson (1991a) reviewed much of the available information and discussed some of the major research needs for the wet tropics forest area. There is some information produced by the QNPWS for the coastal wetlands near Townsville, mostly on the avifauna, and one or two publications on the limnology of the Ross River Dam (e.g. Finlayson & Gillies, 1982). However, these coastal wetlands are not comparable with the natural aquatic habitats in the study area. The ecology of the middle Burdekin River has been studied by a research team at James Cook University, but apart from a short report (Pearson, 1991b) this work remains unpublished. Current studies on fish communities in the Star and Fanning Rivers include sites within the study area, but the work is incomplete and unpublished (B. Pusey, pers. comm.).

Studies of streams in the drier areas comparable with the study area are limited. They include the work on fish communities in the Black River (Beumer, 1980), on catfish populations in Campus Creek, an intermittent stream on James Cook University campus (Orr & Milward, 1984), and on the invertebrate communities of Campus Creek (Smith & Pearson, 1984, 1987).

It is clear, therefore, that the wet/dry forests and woodlands to the west of the wet, coastal ranges have been largely ignored in comparison to the rainforests. Additionally Ridpath (1985) noted that far less research has been conducted into ecological processes of the wet/dry tropics than in temperate or arid regions of Australia. He also pointed out the dangers in trying to apply models from these areas to the wet/dry tropics.

SAMPLING SITES

Terrestrial

Site selection was aimed at replicated sampling of the maximum number of habitat types possible

within the constraints of time, equipment and personnel. The following broad habitat types were identified within the study area from the vegetation map by Power & Jackes (1992) (Fig. 2) and their detailed vegetation descriptions:

CF: closed forest;

TOF: tall open forest or 'wet sclerophyll forest';

OF: open forest;

W: woodland;

R: riverine (riparian) forest;

RK: rocky outcrops;

SW: swamps and other water bodies;

G: grasslands, mostly artificially cleared;

A pilot survey was used to ground-truth the habitat types and to select sampling sites within each broad vegetation type (Fig. 2). Within each of these sites, three or four different sub-sites were selected for intensive sampling. These sub-sites were chosen to maximise the diversity of habitats sampled within each broad vegetation type. The sites were (grid references refer to Australian 1:50 000 topographic maps, series R733):

SITE A: Woodland (W) , vicinity of Dotswood homestead. This site is representative of the large areas of *Eucalyptus crebra* open woodland that cover most of the study area. Three sub-sites were: A1 - riparian vegetation along Keelbottom creek (19°37'S 146°19'E; grid ref. DU 247293); A2 - open woodland with grass understorey (19°36'S 146°17'E; grid ref. DU 227314); and A3 - open woodland with a shrub layer of *Acacia* sp. and grass understorey (19°35'S 146°15'E; grid ref. DU 216330).

SITE B: Woodland (W), between Star homestead and Ponto Hut. This second open woodland site was selected because this vegetation type covered a large proportion of the study area and the fauna might differ between the northern (site B) and southern (site A) areas. Three sub-sites were: B1 - low open *E. shirleyi* woodland with low shrubs along small dry gullies (grid ref. DU 151635); B2 - riparian vegetation (R) along the Little Star river and *E. platyphylla* woodland with dense grass layer (*Heteropogon* sp.)(19°18'S 146°12'E; grid ref. DU 149647); B3 - *E. crebra* open woodland with grassy (*Heteropogon sp.*) understorey (19°19'S 146°18'E; grid ref. DU 206645); B4 - mixed *Eucalyptus* open forest with sparse grass, predominantly *Themeda* sp.

SITE C: Open forest and woodland (OF and W) in the High Range training area. This area consists of denser vegetation than sites A and B with a greater tree diversity. The area is hilly with some rocky outcrops. Four sub-sites were: C1 - *Melaleuca* swamp with sedge and blady grass understorey (19°23'S 146°29'E; grid ref. DU466554); C2 - riparian vegetation along Stake Creek (major tributary of the Fanning river)(19°27'S 146°30'E; grid ref. DU 480481); C3 - Rocky outcrop (19°27'S 146°30'E; grid ref. DU 402482); C4 - open eucalypt forest with grass (*Themeda triandra*) understorey (19°31'S 146°33'E; grid ref. DU 532427).

SITE D: wet sclerophyll forest (TOF) and closed forest (CF) (Bluewater State Forest). This transitional habitat is very narrow and patchy and not readily distinguished in air photos. Dominant tree species are *Syncarpia glomulifera*, *Allocasuarina* sp. and *E. grandis* and there are also several other eucalypts and a variety of rainforest species. The rainforest species often form a shrub layer under the emergent sclerophyll species. This habitat represents an ecotonal area between rainforest and the open eucalypt forest to the west. Three sub-sites were selected on the basis of differing vegetation structure: D1 - closed *Allocasuarina/Syncarpia* forest with dense shrub layer and very little ground cover (19°14'S 146°24'E; grid ref. DU371734); D2 - *Allocasuarina/Syncarpia/Eucalyptus* forest with some shrubs (predominantly rainforest species) and short, dense grass (19°14'S 146°23'E; grid ref. DU 365731); D3 - *Syncarpia/E.grandis/Allocasuarina* forest with dense ground cover of blady grass and sedges and also some patches of dense shrubs (19°14'S 146°23'E; grid ref. DU 359725). D4 - *Allocasuarina/ Eucalyptus* open forest with dense ground cover of *Xanthorrhoea*, *Imperata* and areas of shrubs. *Pandanus* sp. occur in low lying wetter areas. A rainforest sub-site was not sampled due to previous survey work on Mount Halifax which is less than 1km outside the study area (Williams et. al., 1993).

SITE E: open Forest (OF) (19°17'S 146°22'E) on the western side of the Bluewater range. This site is a transitional zone between the dense, wet sclerophyll forest of site D and the eucalypt woodland of site B. The vegetation grades from Tall Open forest with *Eucalyptus grandis*, *Syncarpia glomulifera* and *Allocasuarina torulosa* dominants, through a mixed eucalypt open forest (*E. citriodora, E. peltata, E. shirleyi* and others) to Ironbark woodland near West Keelbottom creek. Riparian vegetation along the creek consists of patches of closed *Tristaniopsis exiliflora* gallery forest and more open *Callistemon* spp./ *Melaleuca* spp. forest. Further upstream there are several vine thickets, which were investigated. The various areas sampled at this site have been combined because of their close proximity and because the site was only sampled once.

Major terrestrial habitat types and associated samples were therefore as follows:

Open woodland: A2, A3, B1, B3

Open forest: B4, C1, C4, D4, E

Tall open forest/closed forest: D1, D2, D3

Riparian: A1, B2, C2, E

TABLE 1. Fish sampling sites and their major physical characteristics. Ref, grid reference, 1:100000 series; Hbt, habitat (P = pool, R = riffle); Temp, temperature (C); D.O., dissolved oxygen (mg/L); Cond, conductivity (µS/cm); Dpth, maximum depth (cm); Wdth, maximum width (m); Subst, major substratum (B = bedrock, RR = large rocks, R = small rocks, G = gravel, S = sand, L = leaf litter; % indicates proportion of substrate damaged by hoofed animals); Curr, current velocity (cm/s); Vegetation: Mel = riparian *Melaleuca* overhanging, W = ironbark woodland, Cal = riparian *Callistemon*, OF = open *Eucalyptus* forest. CF = closed forest.

Site	Ref	Hbt	Temp	D.O.	Cond	pH	Dpth	Wdth	Subst	Curr	Vegetation
1 Star	DU126841	P	22.3	6.7	108	6.9	40	12	RR,R,G,S	3	Mel, wdlnd
		R	22.2	7.1	101	7.0	18	9	R,S	6	Mel, wdlnd
2 Little Star	DU151635	P	19.5	7.0	221	7.4	200	15	R,S		Mel, wdlnd,
		R	19.8	7.0	213	7.1	18	3	R,G,S	15	Mel, wdlnd
3 Star	DU084681	P	-		-	-	-	200	75	S,L	0
				23.6	8.3	-	-	-			
				21.6	11.8	58	8.3 0.3				%
4 Little Star	DU120617	P	20.2	8.8	176	7.6	50	5	R,S,L	0	Melwdlnd
		R	20.5	8.9	163	7.5	15	5	R,S	R,S	-
5 Keelbottom	DU247293	P	22.6	-	420	7.9	30	5		R,S,L	0
		R	22.0	8.4	437	7.9	25	4	RR,R,G,S,L		10
6 Keelbottom	DU301448	P	20.7	7.3	465	7.6	40	3	R,S	0	Mel, OF
		R	21.0	7.9	393	7.7	35	6	R,G,S		30
7 Reid	DU598275	P	28.1	5.1	671	8.6	400	15	B	0	Mel,Cal,OF
		R	26.0	6.8	-	8.1	6	1			R
			23.6	8.3	411	7.7 150		<10%			
8 Fanning	DU421346	P	22.9	7.3	957	8.4	60	10	R,S,L	2	Mel,OF
		R	24.5	7.3	1240	8.8	20	3	R	50	Mel,OF
9 Stake	DU480481	P	22.5	8.1	164	8.4	35	12	R,G,S,L	0	Mel,Cal,OF
10 Little Star	DU334808	P	14.0	11.1	42	-	35	6	R,S,L	0	CF
		R	13.0	10.4	48	7.2	15	5	RR,R,S	20	
11 Keelbottom	DU341786	P	15.5	8.3	42	5.7	25	4	RR,R,S,L	0	CF
		R	14.8	8.0	44	5.4	25	4	R,S	30	CF
			20.0	6.4	37	6.5 180		<10%			
12 Dtswd wetlnd	DU248290		-	-	-	-	-		10-30%		
13 Dtswd dam	DU272272		27.2	9.7	102	8.8	40		30-70%		
14 Dtswd dam	DU275256		24.7	9.2	94	8.5	220		<10%		
15 L.Star Ponto DU244700		21.9	10.7	118	8.2	30				%	
16 Star Stn.dam	DU134605		23.3	8.2	187	8.3 180				%	
17 Star	DU272865		20.0	6.4	37	6.5 180					

Rocky outcrops: C3

Observations were not restricted to these sites, however, and our records are supplemented by information from extensive observations across the study area. For example, while there was only one rocky outcrop sampling site, general observations were made wherever rocky outcrops were encountered, and are incorporated in our composite species lists.

The extent of some habitat types did not warrant

the status of major sites, and were therefore only sampled opportunistically. For example, grassland had mostly been previously cleared land and was not extensive.

Streams

Because of the highly seasonal climate, the streams are seasonal, and surface flow ceases in most of them in the dry season. However, most of the streams have permanent pools. The streams range from upland, rocky, high gradient channels under complete canopy cover to the low gradient, open sandy channels on the south western plain.

Seventeen major sites were selected (Fig. 2) to represent stream and other wetland types across the study area. The grid references and major physical features of the sites are listed in Table 1. In April the streams were running well. In the second survey (September 1991) most streams had ceased to flow and remained only as pools.

The major stream sites were located, from north west to south east, on the Star River (sites 1 and 3), the Little Star River (sites 2, 4 and 10), Keelbottom Creek (sites 5, 6 and 11), Fanning River/ Stake Creek (sites 8 and 9) and Reid River (site 7).

The data in Table 1 broadly illustrate the range of sites sampled, from the low pH, low conductivity, cool rainforest streams in the north (sites 10 and 11) to the warmer, high pH, high conductivity woodland streams in the south east (sites 7, 8 and 9). Differences between the sites reflect several variables, including climate and vegetation, and geology. For example, the streams in the south east included deposits of calcium carbonate in their catchments, which leads to the alkaline water with high conductivity, while those in the rainforest were based on granitic bedrock and soils and had low levels of dissolved substances in them.

SAMPLING METHODOLOGY

Terrestrial Fauna

The sampling strategy was designed to capture or observe the highest diversity of vertebrates possible. Given the time constraints, assessments of absolute densities were given lower priority. A variety of techniques were employed, all of which proved to be useful. Sampling effort was standardised in order to render intersite data as comparable as possible. However, differences in weather, terrain and vegetation all affect the efficiency of sampling. These effects include greater difficulty of observation within dense forest, reduced visibility and/or animal activity during periods of rain or heavy mist, reduction of frog and reptile activity as the weather became cooler and drier, and inability to sample intensively in areas where vehicular access was not possible.

Two surveys were conducted: 8 April-3 May 1991 (site A-D); and 7 August-25 October 1991 (sites A-E). A total of 63 days were spent in the field (approximately 146 person days).

Literature consulted to aid identification were Strahan (1983), Cogger (1986), Hall and Richards (1979), Kitchener and Caputi (1985), Simpson and Day (1984), and Pizzey (1980).

Trapping

Three trapping techniques were utilised:

Elliot traps - 100 elliot traps (type A), divided equally between the sub-sites, were set over three or four nights at each site. Traps were set 10m apart and alternatively baited with oats and vanilla essence, or oats and peanut butter or oats/peanut butter/sardines. These traps are designed for capturing mammals up to the size of rats. Twenty 20 cage traps (bandicoot size) were set with the Elliot traps, equally divided among sub-sites and equally spaced along the trapping lines. These traps were baited with sardines, rolled oats and vanilla essence and were designed to capture medium-sized mammals, e.g. *Isoodon macrourus*. Additionally, 20 large cage traps (cat size) were used at site D in the rainforest. These traps were baited with meat, in an attempt to capture large predators, specifically quolls (*Dasyurus maculatus*), which were known from anecdotal evidence to have occurred at Paluma at least until the 1950's.

Pit traps are suitable for capturing a variety of small mammals, reptiles and amphibians and 30 (20 litre drums) were installed at sites A and B. Five drift fences 10m long and each with two pits were set up at each sub-site (i.e. 10 pits per sub-site × 3 sub-sites = 30 pits and 150m of drift fence per site) at sites A and B. Pit trapping had also been conducted previously in rainforest on Mt Halifax, just outside the study area (Williams et. al., 1993). Pit traps were not used on the other sites because it was found during the first survey of sites A and B that the results were not sufficient to justify the time spent installing them.

Spotlighting

Spotlighting was conducted every night in the field and totalled eight nights per site. Each sub-site was spotlighted at least one night per trip for approximately 1.5hr. Additionally general sur-

TABLE 2. The diversity of vertebrate fauna within the study area. Species previously recorded in the region and which possibly occur within the study area are included (sources of previous records include Lavery & Johnson 1968,1969, Blakers *et. al.* 1984, Winter 1984, Queensland Museum records, QNPWS Mt Spec species list, Garnett (pers. comm.). Sources of possible records are Strahan, 1983; Cogger, 1986; Readers Digest, 1976; Simpson and Day, 1984. Species listed as previously recorded have not necessarily been recorded within the study area, but have been recorded in the near vicinity. Only records of species which are likely to be present (on the basis of available habitat types) have been included.

TAXONOMIC GROUP	OBSERVED	PREVIOUSLY RECORDED/POSSIBLE
MAMMALS		
# Families	18	20
# Species	50	62/76
BIRDS		
# Families	52	66
# Species	180	282/282
REPTILES		
# Families	8	10
# Species	38	64/114
AMPHIBIANS		
# Families	4	4
# Species	16	22/26
FISH		
# Families		
# Species		

veys were conducted at each site. Most of the spotlighting was conducted along tracks using a 150w handheld spotlight from a vehicle, this being the best method for arboreal mammals in the open woodland. Walking transects, using two 30w handheld spotlights and low power torches were conducted in areas inaccessible by vehicle (e.g. along the creeks) and in areas of denser vegetation.

Mist-Netting

Mist netting was undertaken every night in the field to capture bats, but was limited by time and the availability of suitable sites, namely potential flight corridors and water bodies. Netting was conducted for about 2hr commencing at dusk. The nets were usually set above a suitable creek or dam, or across a road (in rainforest at Bluewater). Sites netted were: Keelbottom creek (site A, 19°37'S, 146°17'E; grid ref. DU 247293); Cockatoo dam (site A, 19°34'S, 146°15'E; grid ref. DU 206359); Sandy creek (site A, 19°30'S, 146°15'E; grid ref.DU 215339); Little Star river (site B, 19°18'S, 146°12'E; grid ref. DU 151635); Dinner Creek (site B, 19°23'S, 146°11'E; grid ref. DU 154566); Star River (site B, 19°17'S, 146°07'E; grid ref. DU 081670); Stake Creek (site C, 19°27'S, 146°30'E; grid ref DU 479481); Dip Creek (site C, 19°26'S, 146°32'E; grid ref. DU 509511); Keelbottom creek - Bluewater (site D, 19°14'S, 146°23'E; grid ref. DU 365731); Bluewater forestry road (site D, 19°14'S, 146°24'E; grid ref. DU 375732); unnamed creek (Star 8159-3, 19°30'S, 146°15'E; grid ref. DU 206443).

Birds

Bird species were recorded on a daily basis using several methods. Early morning (dawn) observations were made at each site using both calls and direct observation. Observations were also made while clearing the trapping lines each morning. Each sub-site was also sampled by at least one complete afternoon of bird censusing. Nocturnal birds were recorded using calls and during spotlighting transects. All incidental bird observations were also recorded. Any accessible dams or swamps were visited to record water birds.

Active Searching

Active searching is simply a collective term for a number of activities aimed at finding and capturing cryptic fauna. This includes miscellaneous observations from vehicles or on foot, as well as rolling logs and rocks, searching under bark and inside hollow limbs of dead trees, capturing by hand any lizards or snakes seen, searching hollow trees and under bridges for bats, and searching any piles of tin or timber. These activities are difficult to standardise, but nevertheless are very useful in supplementing species records (especially reptiles).

While every effort was made to standardise sampling within and between sites, it should be noted that spatial and temporal variation in climate, geography and vegetation affected the visibility and/or catchability of different species as well as imposing differing logistic constraints on our sampling routine. For example, at site E, vehicle access was extremely limited and so subsites were much closer together than at other sites.

Fish sampling was done at 11 stream sites and during both surveys, in April and September. Four sampling methods were used:

Seine netting: pools were swept 2-5 times using an 8.0m seine of 10mm mesh. The success of the seine netting was variable, depending on the physical characteristics of the individual pools.

TABLE 3. Number of species of terrestrial vertebrates (excluding feral species) observed during field surveys of the study area by site (habitat).

	SITE A	SITE B	SITE C	SITE D	SITE E
	Ironbark Woodland	Mixed Eucalypt Forest	Wet Sclerophyll Forest	Mixed OF/W	
MAMMALS	27	15	22	16	10
Ex bats	14	11	15	10	8
BIRDS	79	84	82	92	52
Ex open water	79	64	70	90	49
REPTILES	13	8	13	15	8
AMPHIBIANS	9	8	8	4	5
TOTAL	128	115	125	127	75

However, most of the small active fish were recorded using the seine nets.

Fixed net: a 50m fixed net (50mm mesh) was employed at any site which had a large enough pool. The fixed net was useful in catching some of the larger fish and turtles.

Baited lines: baited lines were used in larger pools and were also useful in catching some of the larger species of fish, turtles and eels.

Dip net: weed beds and snags were swept with a hand held dip net to catch small fish such as gudgeons, ambassids, hardyheads and catfish.

Following identification, fish were returned to the water.

In general no voucher specimens were taken. However, specimens of difficult to identify species were taken and checked by dissection (small mammals and fish). The small mammals (*Rattus fuscipes*, *Melomys cervinipes*,and *M. burtoni*) were sent to the Queensland Museum.

RESULTS AND DISCUSSION

A total of 297 species of vertebrates from 91 families were recorded during the fauna surveys. This diversity is not surprising considering the large area and the diversity of habitats included in the area. High diversities of mammals (50 species) and birds (180 species) were recorded, but the diversities of reptiles and amphibians were certainly underestimated because the surveys were conducted outside the wet season. Table 2 summarises the diversity of vertebrate fauna by major taxonomic groups including those species previously recorded in the region and which are likely to occur within the study area.

Table 3 summarises the diversity of terrestrial vertebrates observed by site. In effect, this partly summarises diversity by habitat type, as sites A and B represent Ironbark woodland, site C represents the mixed eucalypt open forest, and sites D and E are a mixture of closed forest and tall open forest (i.e. the transitional zone between rainforest and open forest).

Total numbers of terrestrial vertebrates was surprisingly similar for sites A, B, C and D. The diversity was lowest at site E, but this was primarily due to a lower sampling intensity.

MAMMALS

The 50 species recorded during the surveys (Appendix 1), plus the 11 extra species from other records represent a large proportion (80%) of approximately 76 species that might possibly occur in the area. Mammal diversity was highest in the more open woodland and eucalypt forests of sites A, B and C. This was due to higher observed diversities of bats, arboreal marsupials and macropods in the open forest/woodland sites.

BIRDS

Bird diversity was highest in the wet sclerophyll forest of site D. The higher bird diversity of this forest is especially noticeable if waterbirds are removed from consideration. The number of species recorded during this study (180) (Appendix 1) represents 64% of the 282 species known from all sources to occur in, or in similar habitats close to, the study area. Given (i) the extent and duration of the survey, (ii) the high mobility of birds (which usually leads to a large number of vagrants being recorded in geographical species lists) and (iii) the absence of a number of summer species during the period of field work, this species count is high.

A sighting of a Grey Falcon in open forest at site E was the only observation of a bird listed as rare. Two other rare species previously recorded in the vicinity are the Red Goshawk and Square-tailed Kite. Southern Cassowaries are presently listed as vulnerable.

There are 13 species of bird which are endemic to the north Queensland tropical rainforest (Crome & Nix 1991), and 11 of these were observed during the survey: Mountain Thornbill,

Bridled Honeyeater, Macleay's Honeyeater, Pied Monarch, Bowers Shrike-thrush, Grey-headed Robin, Northern Logrunner, Victoria's Riflebird, Fernwren, Tooth-billed Bowerbird and the Lesser Sooty Owl. An additional species, the Golden Bowerbird, has been previously recorded in the vicinity. Of the 13 species of rainforest endemics, only the Atherton Scrubwren is not likely to be present.

Of ten subspecies endemic to north Queensland (Crome & Nix, 1991) nine were observed within the study area during this study. These were the northern subspecies of King parrot, Pale-yellow Robin, Yellow-breasted Boatbill, Grey Fantail, Eastern Whipbird, Brown Warbler, Northern Catbird, Satin Bowerbird and Boobook Owl (Crome & Nix, 1991).

Reptiles

Reptiles recorded during the study area surveys are listed in Appendix 1. The 38 species observed represent 59% of the 64 species recorded from the study area and its immediate environs. It is likely that a large number of reptile species present in the study area were not recorded because of their cryptic behaviour and lower activity levels in the dry season. Nevertheless, the species list in Tables 6 represent a substantial diversity of reptiles, distributed fairly evenly among wooded habitats.

Amphibians

Amphibian diversity appears to be highest in the open forest/woodland sites, primarily the riparian sub-sites, but this result could change considerably if a wet season amphibian survey was undertaken. Despite the rather poor conditions for observing amphibians, 16 species were recorded for the study area (Appendix 1) with Queensland Museum records increasing the total to 22 species. Most species were recorded in the riparian zones and at dams. However, it is likely that in the early wet season greater numbers of frogs would be observed in the areas away from permanent creeks.

No rare or uncommon species of amphibians were recorded. However, two species of rainforest endemic frogs were recorded (*Cophixalus ornatus* and *Sphenophryne robusta*), and two other species have been recorded previously and are likely to be present (*Nyctimistes dayi* and *Mixophyes schevilli*).

Fish

Fish species recorded in the two surveys are shown in Appendix 1. All, apart from the Eel, are regarded as principal freshwater species, meaning that they undergo their whole life cycle in fresh water. The eel is diadromous, i.e. it has to migrate to the sea to breed.

Diversity at each site varied according to the size of the stream. In the small rainforest streams either no fish were found (site 11) or only the Purple-spotted Gudgeon occurred (site 10). This is similar to the pattern in other rainforest streams: for example, other than the eel, there are no fish in Birthday Creek (R.G. Pearson, unpubl. data) and only the gudgeon in Yuccabine Creek (Pearson et. al., 1986). Further downstream, the sites had a larger complement of fish species with the addition rather than replacement of species - as is the case elsewhere, eg. the Annan River, near Cooktown (Hortle & Pearson, 1990).

It is of interest to compare the diversity of fishes between systems. This is best done using principal freshwater species, and by referencing the sizes of catchment areas, because larger catchments tend to accommodate more species (Welcomme, 1979). The area of the Star catchment sampled was about 1100km^2, that of Keelbottom Creek also about 1100km^2, and that of the upper Fanning River about 200km^2 (Qld Water Res. Comm. data). The fish survey recorded, respectively, 10, 8 and 8 principal freshwater species from these systems, and a total of 11 species. This compares with 12 species in the Black and Alice Rivers (about 300km^2) near Townsville (Beumer, 1980) and 15 species in the Annan River (about 1000km^2) (Hortle & Pearson, 1990). These figures are based on two years' monthly sampling of five sites in the Black/Alice and two sets of samples from 17 sites in the Annan. Comparison with middle Burdekin River samples (Pearson, 1991a) shows that there are only a few extra species recorded or missing from the river.

Given the different sampling intensities and catchment areas of the different systems, it appears that diversity of the fish fauna in the study area compares favourably with other stream systems in northern Queensland. Most of the species recorded have a broad distribution in eastern or northern Australia. Allen (1989) lists species within different status categories (endangered, vulnerable, potentially threatened, indeterminate, restricted and uncertain). The only species to appear on any of these lists and in the records from the study area streams is the Small-headed Grunter, which is listed as restricted. This species is only known from the Burdekin River system. It was not collected during the present survey, but Pusey (pers. comm.) has collected it from Run-

ning River, near the study area, and Pearson (1991b) recorded it from the middle Burdekin River. Otherwise there is no indication of any species of threatened status in the study area. However, samples of gudgeons, provisionally ascribed to *Hypseleotris compressa*, are currently under review.

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APPENDIX 1

Part 1. Mammal species of the study area. The table lists numbers observed during the April/May field trips (nos. before the "/") and the August/September field trips (nos. after the "/"). A - Open woodland (Ironbark) in the southern study area, B - Open woodland (Ironbark) northern study area, C - Open Eucalypt forest (High Range training area), D - Wet sclerophyll/mixed open forest at the R.A.A.F. training area at Bluewater State forest, E - Transitional area between the Wet sclerophyll forest of site D and the open woodland of site B. Observational techniques include E - Elliot traps, C - Cage traps, P - Pits traps, H - by hand, S - spotlighting/miscellaneous observation, F - faecal pellets, M - mist netting, * - presence recorded, but not counted. Species names follow Ingram & Raven (1991).

SPECIES	COMMON NAME		A	B	C	D	E
Tachyglossidae							
Tachyglossus aculeatus	Short-beaked Echidna	S	-/1	-/-	-/-	-/-	-
Dasyuridae							
Antechinus flavipes	Yellow-footed Antechinus	EPHS	-/-	-/-	-/-	2/1	1
Peramelidae							
Isoodon macrourus	Northern Brown Bandicoot	CES	-/-	2/2	1/5	-/3	-
Perameles nasuta	Long-nosed Bandicoot	CS	-/-	-/-	-/-	3/2	2
Phascolarctidae							
Phascolarctus cinereus	Koala	S	-/-	3/-	-/-	-/-	-
Petauridae							
Petaurus breviceps	Sugar Glider	S	1/2	-/1	1/1	-/1	1
Petaurus norfolcensis	Squirrel Glider	S	-/-	-/-	7/2	-/-	-
Pseudocheiridae							
Petauroides volans	Greater Glider	S	3/4	5/10	15/12	-/-	5
Pseudocheirus peregrinus	Common Ringtail Possum	S	-/-	-/-	19/15	-/-	1
Phalangeridae							
Trichosurus vulpecula	Common Brushtail Possum	SC	1/1	1/-	19/17	-/-	3
Potoroidae							
Aepyprymnus rufescens	Rufous Bettong	CS	1/6	3/7	-/-	-/-	1
Macropodidae							
Macropus agilis	Agile Wallaby	S	5/1	-/-	-/-	-/-	-
Macropus giganteus	Eastern Grey Kangaroo	S	6/5+	-/20	2/*	-/-	-
Macropus parryi	Whiptail Wallaby	S	-/2	-/3	-/-	-/-	-
Macropus robustus	Wallaroo	S	-/2	1/-	2/*	-/-	-
Petrogale assimilis	Allied Rock Wallaby	CSF	-/3	-/-	1/5	-/-	-
Wallabia bicolor	Swamp Wallaby	S	-/1	-/-	-/-	-/-	-
Pteropidae							
Nyctimene robinsoni	Queensland Tube-nosed Bat	M	1/-	-/-	-/-	-/-	-
Pteropus alecto	Black Flying-fox	S	1/-	-/*	-/-	-/-	-
Pteropus scapulatus	Little Red Flying-fox	S	-/1	-/*	-/6	-/3	-
Syconycterus australis	Queensland Blossom-bat	M	-/-	-/-	-/-	-/1	-
Mollossidae							
Mormopterus loriae	Little Northern Mastiff-bat	M	3/-	-/-	-/-	-/-	-
Rhinolophidae							
Rhinolophus megaphyllus	Eastern Horseshoe-bat	H	-/-	-/-	-/1	-/-	-
Rhinolophus philipinensis	Large-eared Horseshoe-bat	M	-/-	-/-	-/1	-/-	-
Vespertilionidae							
Chalinolobus gouldii	Gould's Wattled Bat	M	4/4	-/-	-/3	-/-	-
Chalinolobus morio	Chocolate Wattled Bat	M	-/1	-/-	-/-	-/-	-
Chalinolobus nigrogriseus	Hoary Bat	M	3/2	-/-	-/-	-/-	-
Miniopterus australis	Little Bent-wing Bat	M	-/-	-/-	-/1	1/1	-
Miniopterus schreibersii	Common Bent-wing Bat	HM	1/1	-/-	-/2	-/3	-
Myotis adversus	Pond Bat	M	6/-	-/-	-/-	-/2	2
Nyctophilus bifax	North-Queensland Long-eared Bat	M	1/-	-/-	-/1	-/1	2
Nyctophilus geoffroyii	Lesser Long-eared Bat	M	-/-	-/3	-/-	-/-	-
Scoteanax rueppellii	Greater Broad-nosed bat	M	8/-	-/-	-/-	-/-	-
Scotorepens balstoni	Western Broad-nosed bat	M	-/1	-/1	-/-	-/-	-
Scotorepens sanborni	Little Northern Broad-nosed bat	M	-/1	-/1	-/-	-/-	-
Leporidae							
Oryctolagus cuniculus	Rabbit	S	5/2	-/2+	1+/*	-/-	-
Muridae							
Hydromys chrysogaster	Water Rat	CS	3/*	4+/*	2/2	-/1	-
Melomys burtoni	Grassland Melomys	E	-/-	-/-	4/2	3/2	-
Melomys cervinipes	Fawn-footed Melomys	CE	-/-	-/-	9/6	16/12	-
Pseudomys gracilicaudatus	Eastern Chestnut Mouse	E	2/2	1/1	3/2	-/-	-/3
Rattus fuscipes	Bush Rat	EC	-/-	-/-	-/-	28/9	-
Rattus lutreolus	Swamp Rat	E	-/-	-/-	-/-	3/2	-
Rattus rattus	Black Rat	ECS	4/-	-/-	1/1	-/-	-
Uromys caudimaculatus	White-tailed Rat	CSE	-/-	-/-	-/-	5+/-	-
Zyzomys argurus	Common Rock-rat	E	-/-	-/-	4/5	-/-	-
Canidae							
Canis familiaris dingo	Dingo	S	*/*	1/*	1/-	-/-	-
Felidae							

APPENDIX 1 cont.

SPECIES	COMMON NAME		A	B	C	D	E
Felis catus	Feral Cat	S	-/1	-/*	-/-	-/-	-
Equidae							
Equus caballus	Feral Horse	S	-/-	-/-	-/*	-/-	-
Suidae							
Sus scrofa	Feral Pig	SF	*/*	*/*	*/*	*/*	*

Part 2. Bird species of the study area. The index of abundance is based on the following criteria: (-) not observed at this site; 1 - observed on one occasion during the field trip; 2 - observed several times; 3 - common, observed most days; 4 - abundant, observed a number of times every day, usually at several different places. Names follow Ingram & Raven (1991). For further explanation see Part 1.

SPECIES	COMMON NAME		A	B	C	D
Casuariidae						
Casuarius casuarius	Southern Cassowary		-/-	-/-	-/-	-/1
Dromaius novaehollandiae	Emu		-/2	1/2	-/-	-/-
Podicipedidae						
Podiceps cristatus	Crested Grebe					
Poliocephalus poliocephalus	Hoary-headed Grebe		1/-	1/1	-/-	-/-
Tachybaptus novaehollandiae	Australasian Grebe		2/1	1/1	-/1	-/-
Phalacrocoracidae						
Phalacrocorax carbo	Great Cormorant					
Microcarbo melanoleucos	Little Pied Cormorant		-/-	3/1	-/2	-/-
Hypoleucos sulcirostris	Little Black Cormorant		-/-	1/1	-/-	-/-
Anhingidae						
Anhinga novaehollandiae	Australian Darter		-/1	1/1	-/2	-/-
Ardeidae						
Casmerodius alba	White Egret		1/1	1/1	-/-	-/-
Egretta intermedia	Plumed Egret		3/1	2/1	-/-	-/-
Ardea novaehollandiae	White-faced Heron		-/-	-/-	-/3	-/-
Ardea pacifica	White-necked Heron		1/1	1/1	1/-	-/1
Dupetor flavicollis	Black Bittern		1/-	-/-	-/-	-/-
Nycticorax caledonicus	Nankeen Night Heron		-/-	-/1	-/-	-/-2
Theskiornithidae						
Platalea flavipes	Yellow-billed Spoonbill		-/1	-/-	-/-	-/-
Platalea regia	Royal Spoonbill		-/-	-/-	-/1	-/-
Threskiornis spinicollis	Straw-necked Ibis		-/1	2/3	-/1	-/-
Anatidae						
Anas gracilis	Grey Teal		1/-	1/1	-/-	-/-
Anas superciliosa	Black Duck		1/-	3/1	2/2	-/-
Aythya australis	White-eyed Duck		-/1	-/1	-/-	-/-
Chenonetta jubata	Wood Duck		2/-	1/1	1/1	-/-
Dendrocygna arcuata	Wandering Whistling-Duck		2/-	2/1	2/-	-/-
Nettapus coromandelianus	White Pygmy-Goose		1/-	-/1	-/-	-/-
Accipitridae						
Accipiter cirrhocephalus	Collared Sparrowhawk		-/-	-/-	-/-	1/-
Accipiter fasciatus	Brown Goshawk		-/-	-/-	1/1	1/-
Accipiter novaehollandiae	Grey Goshawk		-/-	-/-	-/-	1/1
Aquila audax	Wedge-tailed Eagle		2/2	-/-	2/2	-/-
Aviceda subcristata	Crested Hawk		1/-	3/1	-/-	1/-
Circus assimilis	Spotted Harrier					
Elanus notatus	Black-shouldered Kite		-/1	-/-	1/-	-/-
Haliaeetus leucogaster	White-bellied Sea-Eagle		-/-	1/1	-/-	-/-
Hieraaetus morphnoides	Little Eagle		-/1	-/-	1/-	-/-
Milvus migrans	Fork-tailed Kite		-/-	-/1	1/1	-/-
Haliastur sphenurus	Whistling Kite		1/2	3/3	1/1	-/-
Falconidae						
Falco berigora	Brown Falcon		1/-	1/1	1/1	-/-
Falco cenchroides	Nankeen Kestrel		1/1	1/2	1/2	-/-
Falco hypoleucos	Grey Falcon		-/-	-/-	-/-	-/-
Falco longipennis	Little Falcon		-/-	1/-	-/-	-/-
Megapodiidae						
Alecturi lathami	Brush Turkey		-/-	-/-	-/1	2/1
Phasianidae						
Synoicus australis	Brown Quail		-/-	1/2	1/1	-/1
Gruidae						
Grus rubicundus	Brolga		-/-	1/-	-/-	-/-
Rallidae						
Fulica atra	Eurasian Coot		1/1	-/1	-/-	-/-
Gallinula tenebrosa	Dusky Moorhen		1/1	1/1	-/1	-/-
Rallina tricolor	Red-necked Crake		-/-	-/-	-/-	-/1
Otididae						
Ardeotis australis	Australian Bustard		-/-	-/-	1/1	-/-
Jacanidae						
Irediparra gallinacea	Comb-crested Jacana		1/-	1/1	-/-	-/-
Burhinidae						
Burhinus grallarius	Bush Thick-knee		2/-	-/1	1/2	-/2
Charadriidae						
Elseornis melanops	Black-fronted Plover		1/-	-/-	-/-	-/-
Vanellus miles	Masked Lapwing (Plover)		1/-	-/3	1/-	-/-
Columbidae						
Chalcophaps indica	Green-winged Pigeon		-/-	-/-	-/-	-/2
Columba leucomela	White-headed Pigeon		-/-	-/-	-/-	1/-
Geopelia placida	Peaceful Dove		-/-	2/3	3/3	-/-
Ocyphaps lophotes	Crested Pigeon		4/-	4/4	1/1	-/-
Petrophassa scripta	Squatter Pigeon		-/-	2/3	1/1	-/-

APPENDIX 1 cont.

SPECIES	COMMON NAME		A	B	C	D
Todirhamphus macleayii	Forest Kingfisher		-/-	-/-	2/2	-/2
Todirhamphus pyrrhopygius	Red-backed Kingfisher		-/-	1/-	-/-	-/-
Todirhamphus sanctus	Sacred Kingfisher		1/-	1/-	-/1	-/-
Meropidae						
Merops ornatus	Rainbow Bee-eater		2/-	-/-	3/-	1/3
Pittidae						
Pitta versicolor	Noisy Pitta		-/-	-/-	-/-	1/2
Campephagidae						
Coracina novaehollandiae	Black-faced Cuckoo-Shrike		2/2	3/1	3/2	-/1
Coracina papuensis	Little Cuckoo-Shrike		2/3	1/-	-/1	1/2
Lalage leucomela	Varied Triller		-/-	-/-	-/-	1/1
Orthonychidae						
Orthonyx spaldingii	Northern Logrunner		-/-	-/-	-/-	3/2
Psophodes olivaceus	Eastern Whipbird		-/-	-/-	-/-	4/2
Pomatostomidae						
Pomatostomus temporalis	Grey-crowned Babbler		1/3	1/2	-/-	-/-
Sylviidae						
Cinclorhamphus mathewsi	Rufous Songlark		2/1	1/-	-/-	-/-
Megalurus timoriensis	Tawny Grassbird		-/-	-/-	-/-	-/-
Maluridae						
Malurus melanocephalus	Red-backed Wren		1/-	-/-	3/3	-/2
Acanthizidae						
Acanthiza katherina	Mountain Thornbill		-/-	-/-	-/-	1/-
Acanthiza nana	Little Thornbill		1/3	1/2	-/-	-/-
Oreoscopus gutturalis	Fernwren		-/-	-/-	-/1	-/-
Gerygone fusca	Western Warbler		1/-	-/-	-/-	-/-
Gerygone mouki	Brown Warbler		-/-	-/-	-/-	3/-
Gerygone olivacea	White-throated Warbler		-/-	-/1	-/1	-/-
Gerygone palpebrosa	Fairy Warbler		-/-	-/-	-/1	1/1
Sericornis citreogularis	Yellow-throated Scrubwren		-/-	-/-	-/-	-/1
Sericornis frontalis	White-browed Scrubwren		-/-	-/-	-/-	1/1
Sericornis magnirostris	Large-billed Scrubwren		-/-	-/-	-/-	1/1
Monarchidae						
Arses kaupi	Pied Monarch		-/-	-/-	-/-	4/1
Machaerirhynchus flaviventer	Yellow-breasted Boatbill		-/-	-/-	-/-	1/1
Monarcha trivirgatus	Spectacled Monarch		-/-	-/-	-/1	4/3
Myiagra cyanoleuca	Satin Flycatcher		-/-	-/-	1/1	1/-
Myiagra rubecula	Leaden Flycatcher		-/-	1/-	1/4	-/2
Rhipidura fuliginosa	Grey Fantail		4/4	4/3	4/4	4/2
Rhipidura leucophrys	Willie Wagtail		3/3	4/3	2/-	-/-

SPECIES	COMMON NAME		A	B	C	D
Macropygia phasianella	Brown Pigeon		-/-	-/-	-/-	1/-
Phaps chaloptera	Common Bronzewing		-/2	1/-	-/-	-/-
Ptilinopus magnificus	Wompoo Pigeon		-/-	-/-	-/-	-/2
Ptilinopus superbus	Purple-crowned Pigeon		-/-	-/-	-/-	-/2
Loriidae						
Trichoglossus chlorolepidotus	Scaly-breasted Lorikeet		-/-	-/-	1/2	-/2
Trichoglossus haematodus	Rainbow Lorikeet		3/4	1/3	3/3	1/3
Cacatuidae						
Cacatua galerita	Sulphur-crested Cockatoo		3/3	4/3	-/1	1/3
Calyptorynchus magnificus	Red-tailed Black Cockatoo		1/1	-/-	1/-	2/1
Psittacidae						
Alisteris scapularis	King Parrot		-/-	-/-	-/-	-/1
Aprosmictus erythropterus	Red-winged Parrot		1/2	1/1	-/1	-/-
Platycerus adscitus	Pale-headed Rosella		3/2	4/3	3/2	-/-
Platycerus elegans	Crimson Rosella		-/-	-/-	-/-	1/-
Cuculidae						
Centropus phasianinus	Pheasant Coucal		2/1	3/3	2/1	-/1
Chrysococcyx basalis	Horsfield's Bronze-Cuckoo		-/-	-/-	-/1	1/-
Chrysococcyx russatus	Rufous-breasted Bronze-Cuckoo		-/-	-/-	-/-	1/-
Chyrsococcyx lucidus	Shining Bronze-Cuckoo		-/-	-/-	-/-	1/-
Cacomantis flabelliformis	Fantail Cuckoo		-/-	1/1	1/-	4/2
Tytonidae						
Tyto alba	Barn Owl		-/1	-/-	-/-	-/1
Tyto multipunctata	Lesser Sooty Owl		-/-	-/-	-/-	1/2
Strigidae						
Ninox connivens	Barking Owl		-/-	-/1	-/-	-/1
Ninox boobook	Boobook		2/2	-/1	-/-	-/1
Podargidae						
Podargus papuensis	Papuan Frogmouth		-/-	-/-	-/-	1/-
Podargus strigoides	Tawny Frogmouth		-/1	1/1	-/1	-/-
Aegothelidae						
Aegotheles cristatus	Australian Owlet Nightjar		2/-	3/1	-/-	-/-
Caprimulgidae						
Caprimulgus macrurus	Large-tailed Nightjar		-/-	-/-	-/-	-/2
Eurospododus mystacalis	White-throated Nightjar		-/-	-/-	-/-	-/2
Eurostopodus argus	Spotted Nightjar		-/1	-/-	1/-	-/-
Alcedinidae						
Ceyx azureus	Azure Kingfisher		2/-	3/1	1/3	1/1
Ceyx pusillus	Little Kingfisher		-/-	1/1	-/-	-/1
Dacelo leachii	Blue-winged Kookaburra		1/-	-/3	1/3	-/-
Dacelo novaeguineae	Laughing Kookaburra		3/2	3/3	2/3	-/2

APPENDIX 1 cont.

SPECIES	COMMON NAME		A	B	C	D
Melaphaga notata	Yellow-spotted Honeyeater		-/-	-/-	-/1	1/1
Melaphaga lewinii	Lewins Honeyeater		-/-	-/-	-/-	4/3
Melithreptus albogularisi	White-throated Honeyeater		2/4	4/2	4/4	-/-
Melithreptus lunatus	White-naped Honeyeater		-/-	-/-	-/-	-/1
Myzomela obscura	Dusky Honeyeater		-/-	-/1	-/1	-/3
Myzomela sanguinolenta	Scarlet Honeyeater		-/1	-/1	1/1	-/3
Philemon argenticeps	Silver-crowned Friarbird		1/-	-/-	-/-	-/-
Philemon citreogularis	Little Friarbird		-/4	-/3	-/-	-/-
Philemon corniculatus	Noisy Friarbird		-/4	-/3	-/3	-/-
Ramsayornis modestus	Brown-backed Honeyeater		-/-	-/-	-/2	-/-
Xanthotis macleayana	Macleay's Honeyeater		-/-	-/-	-/-	2/2
Estrildidae						
Lonchura punctulata	Spice Finch		-/-	1/-	-/-	-/-
Neochmia temporalis	Red-browed Finch		-/-	-/-	3/3	1/-
Taeniopygia bichenovii	Double-barred Finch		1/-	-/-	-/-	-/-
Oriolidae						
Oriolus sagittatus	Olive-backed Oriole		-/1	1/-	-/-	3/1
Dicruridae						
Dicrurus bracteatus	Spangled Drongo		-/-	-/1	1/-	-/1
Grallinidae						
Grallina cyanoleuca	Peewee		3/4	4/3	2/3	-/-
Corcoracidae						
Corcorax melanorhamphos	White-winged Chough		-/-	2/1	1/2	-/-
Struthidea cinerea	Apostlebird		4/2	2/2	-/1	-/-
Artamidae						
Artamus leucorhynchus	White-breasted Woodswallow		-/-	-/1	-/-	1/1
Cracticidae						
Cracticus nigrogularis	Pied Butcherbird		2/3	4/4	1/2	-/-
Cracticus torquatus	Grey Butcherbird		3/3	3/3	1/2	-/-
Gymnorhina tibicen	Australian Magpie		4/4	4/4	3/4	-/-
Strepera graculina	Pied Currawong		1/1	1/1	3/3	2/2
Ptilonorhychidae						
Ailuroedus melanotis	Spotted Catbird		-/-	-/-	-/-	1/-
Chlamydera nuchalis	Great Bowerbird		3/1	1/-	-/1	-/-
Ptilonorhynchus violaceus	Satin Bowerbird		-/-	-/-	-/-	1/-
Paradisaeidae						
Ptiloris victoriae	Victoria's Riflebird		-/-	-/-	-/-	3/3
Corvidae						

SPECIES	COMMON NAME		A	B	C	D
Rhipidura rufifrons	Rufous Fantail		-/-	-/-	-/-	1/3
Eopsaltridae						
Eopsaltria australis	Eastern Yellow Robin		-/-	-/-	-/1	4/3
Heteromyias cinereifrons	Grey-headed Robin		-/-	-/-	-/-	1/1
Microeca flavigaster	Lemon-breasted flycatcher		-/-	-/-	-/3	-/-
Microeca leucophaea	Jacky Winter		2/-	-/-	-/-	-/-
Tregellasia capito	Pale-yellow Robin		-/-	-/-	-/-	2/3
Pachycephalidae						
Colluricincla boweri	Bowers Shrike-Thrush		-/-	-/-	-/-	1/-
Colluricincla harmonica	Grey Shrike-Thrush		-/-	-/-	-/-	2/1
Colluricincla megarhyncha	Rufous Shrike-Thrush		-/-	-/-	-/-	4/4
Pachycephala pectoralis	Golden Whistler		-/-	-/-	-/-	4/3
Pachycephala rufiventris	Rufous Whistler		2/4	1/2	4/4	1/1
Neosittidae						
Daphoenositta chrysoptera	Sittella		-/-	-/-	-/-	1/-
Climacteridae						
Climacteris picumnus	Brown Treecreeper		-/-	1/-	-/-	-/-
Cormobates leucophaea	White-throated Treecreeper		-/-	-/-	-/-	4/3
Dicaeidae						
Dicaeum hirundinaceum	Mistletoebird		-/1	-/-	-/-	3/1
Pardalotidae						
Pardalotus punctatus	Spotted Pardalote		-/-	-/-	-/-	2/1
Pardalotus striatus	Striated Pardalote		4/4	4/4	4/3	2/-
Zosteropidae						
Zosterops lateralis	Silvereye		-/-	-/-	-/-	3/3
Meliphagidae						
Acanthorhynchus tenuirostris	Eastern Spinebill		-/-	-/-	-/-	-/1
Cissomela pectoralis	Banded Honeyeater		-/-	-/-	-/2	-/-
Entomyzon cyanotis	Blue-faced Honeyeater		4/4	3/3	2/2	-/-
Meliphaga chrysops	Yellow-faced Honeyeater		-/-	-/-	-/-	1/3
Meliphaga flavescens	Yellow-tinted honeyeater		-/-	-/-	-/-	-/-
Meliphaga flava	Yellow Honeyeater		-/-	-/-	1/-	-/-
Meliphaga frenata	Bridled Honeyeater		-/-	-/-	-/-	-/1
Meliphaga fusca	Fuscous honeyeater		-/-	-/-	-/-	-/-
Lichmera indistincta	Brown Honeyeater		-/-	-/1	1/3	1/2
Manorina flavigula	White-rumped Miner		2/4	4/3	-/-	-/-
Manorina melanocephala	Noisy Miner		2/3	2/4	-/3	-/-

APPENDIX 1 cont.

SPECIES	COMMON NAME		A	B	C	D
Corvus coronoides	Australian Raven		-/3	-/-	-/-	-/-
Corvus orru	Australian Crow		4/3	4/3	3/3	-/2

Part 3. Reptiles of the study area. The index of abundance is based on the following criteria : (-) not recorded at this site; 1 - observed once during the field trip; 2 - observed several times; 3 - common, observed most days; 4 - abundant, observed a number of times every day, usually at several locations. For further explanation see Part 1. Species names follow Ingram & Raven (1991).

SPECIES	COMMON NAME		A	B	C	D	E
Gekkonidae							
Diplodactylus steindachneri		HP	1/1	-/-	-/-	-/-	HP
Gehyra dubia		H	-/1	2/1	1/1	-/-	-
Heteronotia binoei	Bynoe's Gecko	H	3/3	-/2	2/2	-/-	-
Oedura castlenaui	Northern Velvet Gecko	H	-/-	2/2	-/-	-/-	-
Scincidae							
Carlia rostralis		H	-/-	-/-	-/-	-/-	1
Carlia jarnoldae		H	-/-	-/-	-/1	-/1	1
Carlia munda	HP	1/1	-/-	2/2	-/-	-	
Carlia mundivensis		H	-/1	-/-	2/2	-/-	-
Carlia rubigularis		H	-/-	-/-	-/-	3/3	-
Cryptoblepharus virgatus		H	3/-	2/2	2/2	-/-	2
Ctenotus spaldingi		H	-/-	-/-	-/-	-/1	-
Egernia striolata	Tree Skink	H	-/-	1/-	-/-	-/-	-
Sphenomorphus quoyii	Water Skink	SH	-/-	-/-	-/-	1/2	-
Lampropholis basiliscus		H	-/-	-/-	-/-	1/1	-
Lygisaurus foliorum		H	-/-	-/-	-/-	-/1	-
Menetia greyii		HP	1/1	-/-	-/-	-/-	-
Morethia taeniopleura	Fire-tailed Skink	HP	3/1	-/-	3/2	-/-	-
Agamidae							
Pogona barbata	Bearded Dragon	HS	-/-	1/1	-/-	-/-	-
Diporiphora australis	Two-line Dragon	HS	-/-	-/-	1/1	-/-	-
Physignathus lesueurii	Water Dragon	HS	-/-	-/-	-/-	2/1	1
Varanidae							
Varanus scalaris	Spotted Tree-monitor	H	1/-	-/-	-/-	-/2	-
Varanus varius	Lace Monitor	H	-/-	-/-	-/1	-/1	1
Boidae							
Aspidites melanocephalus	Black-headed Python	H	1/-	-/-	-/-	-/—	
Morelia amethistina	Amethystine Python	H	-/-	-/-	-/-	1/-	-
Morelia maculosa	Childrens Python	HS	2/-	-/-	-/-	-/-	-
Colubridae							
Tropidonophis mairii	Keelback	H	-/-	-/-	-/1	-/-	1
Dendrelaphis punctulata	Common Tree Snake	H	-/-	-/-	-/-	1/22	
Elapidae							
Demansia vestigiata	Black Whipsnake	S	-/-	-/-	1/-	-/-	-
Demansia psammophis	Yellow-faced Whipsnake	H	-/-	-/-	-/-	1/22	
Furina ornata	Orange-naped Snake	H	-/1	-/-	-/-	-/-	-
Pseudechis porphyriacus	Red-bellied Black Snake	SH	-/-	-/-	-/-	3/3	-
Pseudonaja textilis	Eastern Brown Snake	HS	2/-	-/-	-/-	-/-	-
Rhinoplocephalus nigrescens	Small-eyed Snake	H	-/-	-/-	-/-	-/1	-
Chelidae							
Elseya latisternum	Sawshell Tortoise	H	-/-	1/2	2/2	-/-	-
Emydura krefftii	Krefft's River Tortoise	H	-/-	1/2	1/1	-/-	-

Part 4. Frogs of the study area. Species names follow Ingram & Raven (1991). For further explanation see Part 1.

SPECIES	COMMON NAME		A	B	C	D
Bufonidae						
Bufo marinus	Cane Toad	HSP	4/4	4/4	4/4	4/4
Hylidae						
Cyclorana novaehollandiae		H	2/-	-/-	-/-	-/-
Litoria alboguttata	Green-stripe Frog	H	2/-	-/-	-/-	-/-
Litoria caerulea	Green Tree Frog	HSP	2/-	1/-	1/-	1/-
Litoria inermis		HS	3/3	3/3	1/1	-/-
Litoria latopalmata		H	-/-	-/-	-/2	-/-
Litoria leseuri	Stony-creek Frog	HSP	-/-	3/3	3/3	3/3
Litoria nasuta	Striped Rocket Frog	HS	-/-	-/2	2/-	3/3
Litoria rothii	Red-eyed Tree Frog	H	1/1	1/-	-/-	-/-
Litoria rubella	Naked Tree Frog	PH	3/-	-/-	-/-	-/-
Myobatrachidae						
Limnodynastes ornatus	Ornate Burrowing Frog	PHS	4/2	1/1	2/-	-/—
Limnodynastes peronii	Striped Marshfrog Frog	H	-/-	-/2	-/-	-/-2
Limnodynastes tasmaniensis	Spotted Marshfrog	H	-/-	-/-	1/-	-/-
Uperoleia lithomoda/mimula		PH	3/-	-/-	-/-	-/-

APPENDIX 1 cont.

Part 5. Fish of the study area. An abundance index indicates the number of individuals caught per sample as follows: -, not observed at this site; 1, observed at least once during each sampling period; 2, observed several times during sampling period; 3, observed regularly and caught in most seine sweeps; 4, caught in every seine sweep usually in large numbers. Species names follow Allen (1989). "Burd" and "Pus" refer to species recorded by other workers (see text). No samples taken at sites 7, 8 & 9 in second trip. Catchments are S, Star; K, Keelbottom; F, Fanning; and R, Reid.

	1	2	3	4	5	6	7	8	9	10	11	Burd	Pus
Catchment: S	S	S	S	K	K	R	F	F	S	K			F&K
Family Anguillidae													
Anguilla reinhardtii (Eel)	-/-	1/-	1/-	-/-	-/-	-/-	-/	-/	-/	-/-	-/-	Y	-
Family Clupeidae													
Nematolosa erebi (Bony bream)	-/1	-/1	4/1	3/1	-/-	3/3	-/	3/	-/	-/-	-/-	Y	Y
Family Ariidae													
Arius graeffei (Salmon catfish)	-/-	-1-	-/-	-/-	-/-	-/-	-/	-/-	-/	-/-	-/-	Y	-
Family Plotosidae													
Neosilurus hyrtlii (Hyrtl's tandan)	-/-	1/-	-/-	-/2	-/-	-/2	-/	2/	-/	-/-	-/-	Y	Y*
Family Belonidae													
Strongylura kreffiii (Freshwater longtom)	-/-	-/-	-/-	-/-	-/-	-/-	-/	-/	-/	-/-	-/-	Y	-
Family Melanotaeniidae													
Melanotaenia s. splendida (Australian rainbow fish)	4/4	4/4	4/4	4/4	4/4	4/4	2/	4/	4/	-/-	-/-	Y	Y
Family Atherinidae													
Craterocephalus stercusmuscarum (Fly-specked hardihead)	4	-/4	3/2	1/4	-/-	-/-	-/	-/	-/	-/-	-/-	-	Y
Family Ambassidae													
Ambassis agassizi (Agassiz's glassfish)	-/2	2/-	-/-	1/2	-/-	1/4	-/	-/	3/	-/-	-/-	-	Y
Family Teraponidae													
Leiopotherapon unicolor (Spangled perch)	-/-	2/3	2/3	2/-	2/3	3/4	-/	-/	-/	-/-	-/-	Y	Y
Amniataba percoides (Barred grunter)	-2	2/3	2/3	-/3	2/-	2/-	1/	1/	-/	-/-	-/-	Y	Y
Hephaestus fuliginosus (Sooty grunter)	2/2	2/2	-/2	-/-	-/-	-/-	2/	-/	-/	-/-	-/-	Y	Y
Scortum parviceps (Small-headed grunter)	-/-	-/-		-/-	-/-	-/-	-/-	-/	-/	-/	-/-	-/-	Y
Family Apogonidae													
Glossamia aprion (Mouth almighty)	-/-	-/-	-/-	-/-	-/-	-/-	-/	-/	-/	-/-	-/-	Y	-
Family Toxotidae													
Toxotes chatareus (Seven-spot archerfish)	-/-	-/-	-/-	-/-	-/-	-/-	-/	1/	-/	-/-	-/-	Y	Y
Family Eleotridae													
Mogurnda adspersa (Purple-spotted gudgeon)	2/2	2/2	3/2	2/2	2/2	2/3	-/	-/	2/	2/-	-/-	-	Y
?*Hypseleotris compressa* (Empire gudgeon)	1/-		1/-		1/-	-/-	1/-	1/2	-/	1/	4/	-/-	-/-
Philypnodon grandiceps (Flathead gudgeon)	-/-	-/-	-/-	-/-	-/-	-/-	-/	-/	-/	-/-	-/-	Y	-
Family Gobiidae													
Glossogobius ?giurus (Flathead goby)	-/-	-/-	-/-	-/-	-/-	-/-	-/	-/	-/	-/-	-/-	Y	-

VERTEBRATE FAUNA OF THREE MOUNTAIN TOPS IN THE TOWNSVILLE REGION, NORTH QUEENSLAND: MOUNT CLEVELAND, MOUNT ELLIOT AND MOUNT HALIFAX

STEVE WILLIAMS, RICHARD PEARSON AND SCOTT BURNETT

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Vertebrate fauna surveys were carried out on the summits of Mount Cleveland, Mount Elliot and Mount Halifax in north Queensland. The main focus was on mammals and birds, but observations on all vertebrate groups are included. Habitats included rainforest and open eucalypt/casuarina forest. The surveys recorded a total of 136 species of vertebrates including 17 mammal, 77 bird, 32 reptile and 10 frog species. Habitat descriptions and measures of relative abundance for mammals and birds are included. □ *Survey, vertebrate, mountain, north, Queensland, Australia.*

Steve Williams, Richard Pearson & Scott Burnett, Australian Centre for Tropical Freshwater Research, James Cook University of North Queensland, Queensland 4811, Australia; 15 November, 1992.

This paper reports the findings of vertebrate fauna surveys conducted on three mountain tops in the Townsville region of north Queensland. Most of the effort of the survey was directed at mammal and bird communities. However, all vertebrates were recorded and the data are included here. Reptiles, amphibians and invertebrates are dealt with in detail by Graham (1991). The fauna surveys were part of multidisciplinary fieldwork examining the suitability of Mount Elliot, Mount Cleveland and Mount Halifax for the placement of a radar tower by the Civil Aviation Authority.

Mountain top habitats are usually restricted and isolated from other patches of similar habitat. As well, there are usually endemic species associated with these restricted areas of habitat and, because endemic species were of special concern, fieldwork was mostly concentrated on the summit and the high ridges and saddles of the mountains.

The primary aim of the surveys was to provide a baseline description of the fauna of these mountain tops. Therefore, sampling was designed to record the presence of as many species as possible. This was achieved by using a variety of techniques in as many different micro-habitats (or habitat patches) as possible. Intensive sampling was conducted in each patch of different habitat within each study area. Selection of specific subsites was primarily based on vegetation, topography and substrate types. The vegetation classifications used were those of Walker & Hopkins (1990). Each mountain was sampled twice, during the early wet season (December 1990) and again in the early dry season (April 1991).

Previous mammal and bird surveys were carried out in the area by Lavery (1968) (birds), Lavery & Johnson (1968) (mammals), Lavery & Johnson (1974) (mammals) and Lavery & Seton (1974) (birds).

SITE DESCRIPTIONS

MOUNT CLEVELAND

Mount Cleveland (19°20'S, 147°03'E) is situated within Bowling Green Bay National Park, approximately 25km east of Townsville (Fig. 1). At 558m it is substantially lower than other mountains in the vicinity. Average annual rainfall is approximately 1000mm most of which occurs during the months December to March.

The vegetation at the summit of Mount Cleveland primarily consists of a relatively dense tree layer of *Allocasuarina torulosa* and mixed eucalypts, a dense middle layer of *Xanthorrhoea johnsonii* and a ground layer dominated by Blady Grass (*Imperata cylindrica*), over a rocky substrate.

Sub-sites selected for intensive sampling on Mount Cleveland were (topographic map used was Bowling Green 1:50 000, Sheet 8359-111, Edition 1-AAS, Series R 733):

C1 Mount Cleveland summit (Grid ref. 030706, altitude 558m): Mammal traps were laid in a circle around the summit ridge. The terrain was steep with large boulders and rock overhangs. Vegetation classification: very tall *Xanthorrhoea* shrubland above tall grassland (X4V/G3M). There was also dense vegetation, including some

rainforest taxa, in the gaps between the large boulders.

C2 Saddle between camp and summit (Grid ref. 033708, altitude 480m): the saddle was mostly flat with relatively few rocky outcrops. Vegetation classification: *Allocasuarina torulosa* dominated mid-high open forest with sclerophyll emergents over a very tall *Xanthorrhoea johnsonii* dominated shrubland (ALTOR ET6M/X4S). There were also patches of dense Blady Grass (*Imperata cylindrica*) in the more open areas.

C3 Rainforest (Grid ref. 034706, altitude 460m): Rainforest (c.2ha) was present in the catchment area of several rocky gullies just to the south of site C2. Vegetation classification: simple notophyll mixed tall closed forest (T7D S5M6).

C4 Rocky ridge (Grid ref. 036710, altitude 470m): The area was very rocky with outcrops of large granite boulders. The vegetation here is classified the same as site C2 (ALTOR ET6M/X4S), but it was much more rocky, the *Xanthorrhoea* was not as dense, and there were no significant areas of Blady Grass.

Mount Elliot

Mount Elliot (19°30'S, 146°57'E) is situated approximately 30km south-east of Townsville (Fig. 1) and, with an elevation of 1221m, is the highest mountain in the Townsville region. The group of mountains associated with Mount Elliot runs almost due north-south and hence they are influenced by the southeasterly trade-winds which blow up the Queensland coast. The area receives approximately 1200mm of rainfall annually, although the mountain top could be expected to receive considerably more than this due to its greater elevation. The majority of rainfall occurs during the months December to March.

Mount Elliot is entirely within Bowling Green Bay National Park and appears on the register of the National Estate. Unlike most areas to the north, Mount Elliot appears not to have been logged and, hence, remains relatively undisturbed. The rainforest on Mount Elliot is not contiguous with the northern forest and represents an island of forest surrounded by dry open woodland.

Sub-sites selected for intensive sampling on Mount Elliot were (topographic map used was Mount Elliot (Special), Edition 1, Series R733, 1:50 000.):

E1 (Grid ref. 109582, Altitude 1200m): narrow, steep summit ridge with Simple notophyll tall mixed closed forest with *Archontophoenix alexandrae* emergents (AT7D S5M6). This area was typical of the summit with a rocky substrate and a well developed understorey vegetation.

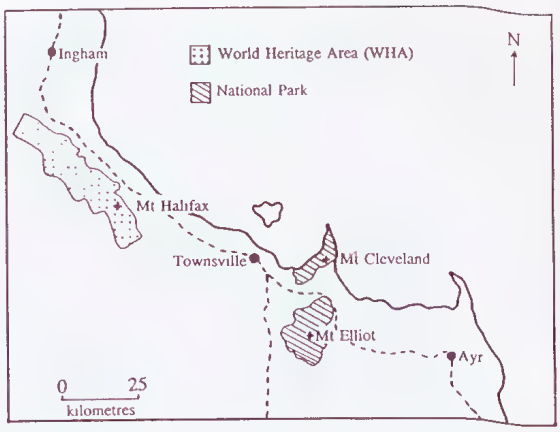

FIG.1. Map of Townsville region showing the locations of the study sites.

E2 (Grid ref. 109581, Altitude 1200m): ridge top clearing, classified as Dwarf closed vineland with *Archontophoenix alexandrae* and *Cyathea sp.* emergents (AL4D). This site was representative of a number of similar clearings near to the summit of Mount Elliot, with a very dense ground cover of vines and scramblers about 1m thick. There is virtually no canopy except an occasional palm.

E3 (Grid ref. 112576, Altitude 1150m): wide ridge top with Simple notophyll mixed very tall closed forest (T8D S5M2). The vegetation at this site has a more open understorey than site E1.

E4 (Grid ref. 114574, Altitude 1150m): headwaters of eastern catchment area. The forest here was taller with fewer small saplings and a distinctive middle layer of the tree fern *Cyathea rebeccae*. Classification was Simple notophyll mixed very tall closed fern forest (T8D S5M2).

Mount Halifax

Mount Halifax (19°07'S, 146°22'E), situated 50km west north-west of Townsville (Fig. 1), is the highest mountain, at 1064m, in the Paluma Range. It is a very wet area and the average annual rainfall for the region is approximately 2600mm, with the majority falling during the period December to March.

Sub-sites selected for intensive sampling were (Map used was Rollingstone, Series R733, Sheet 8159 1, Edition 3-AAS 1:50 000):

H1 (Grid ref. 341862, Altitude 1020m): wet, ridge-top rainforest (very wet due to almost continuous cloud drip) - the SE ridge from the summit.

Vegetation Classification: Simple Notophyll Mixed Tall Closed Forest T7D S5M6.

H2 (Grid ref. 340863, Altitude 1040m): drier rainforest on the western slope of the SE ridge. Vegetation classification: T7D S5M6.

H3 (Grid ref. 344861, Altitude 1020m): taller rainforest on narrow ridge and saddle SE of camp. Vegetation classification: Simple Notophyll Mixed Very Tall Closed Forest T8D S5M6.

H4 (Grid ref. 342862, Altitude 1040m): heath vegetation near summit ridge. Vegetation classification: mid-high *Leptospermum amboinense* Open Forest above a tall sparse heathland and mid-high closed forbland LEAMB T6M/Z4V/F2D.

H5 (Grid ref. 339864, Altitude 1060m): dense, low sclerophyllous vegetation on summit. Vegetation classification: Dwarf *Callistemon viminalis* closed forest with sclerophyll emergents above a mid-high closed forbland (ET4D/F2D).

METHODS

Identification

Voucher specimens of mammals, reptiles and amphibians that were difficult to identify were collected and lodged with the Queensland Museum (mammals) or with Queensland National Parks and Wildlife Service (reptiles and amphibians). Catalogue numbers are as yet unavailable as not all of the material has been sorted. Species worthy of special mention here are those bird observations which are range extensions (Victoria Riflebird, *Ptiloris victoriae*, Grey-Headed Robin, *Heteromyias cinereifrons*, Bridled Honeyeater, *Meliphaga frenata*, and Bower's Shrike-Thrush, *Colluricincla boweri*), and the small mammals *Rattus fuscipes* and *Melomys cervinipes*. No voucher specimens of birds were taken. Observations of Grey-Headed Robins and Bridled Honeyeaters were numerous and reliable, however only one sighting was made of Victoria's Riflebird and Bower's Shrike-thrush. *Rattus fuscipes* is very similar to *R. leucopus*. However, several skulls were examined from Mount Halifax and Mount Elliot and these proved to be *R. fuscipes*. In addition, two adult females on Mount Elliot had eight nipples (*R. fuscipes* has eight nipples while *R.leucopus* has six). As well, several specimens of *Melomys cervinipes* were identified on the basis of molar dentition and in the field on weight, fur texture and fur colour. The average weight of *M.cervinipes* on Mount Cleveland was 85g with an adult range of 70-115g. This differs from the range of 45-65g for *M.burtoni* (Strahan, 1983). Obviously these identifications do not preclude the possibility of either *Rattus leucopus* or *Melomys burtoni* being present. Also there is considerable evidence showing that in north Queensland *M. cervinipes* is a forest generalist rather than a closed forest specialist and has much broader habitat preferences than previously thought (Winter et. al., 1984; Williams, unpub. data).

Mammal Trapping

All of the sub-sites were trapped for four consecutive nights on each trip. Sub-sites C1, C2, C3 and C4 (Mount Cleveland) and sub- sites E1, E2, E3 and E4 (Mount Elliot) all had 25 Elliot "type A" traps and five wire cage "bandicoot" traps. Sub-sites H1, H2 and H3 (Mount Halifax) had 20 Elliot traps, while sub-site H4 and H5 had 10 Elliot traps and two cage traps. Traps were placed at 10m intervals with cage traps equally spaced along the transect. Traps were baited with a mixture of rolled oats, peanut butter and vanilla essence. Cage traps were also baited with sardines to attract carnivores (e.g. quolls). Two drift fence/pit trap lines were set up at Mount Elliot and Mount Halifax. Each drift fence consisted of 50m of fence (30cm high) with six pit traps (20 litre plastic drums) at about 7m intervals.

Data collected from trapped animals included species, sex, reproductive status and weight. Each animal was marked with a small notch in the right ear and then released.

Bird Observations

A walking transect (c.20min) was conducted at each sub- site for four consecutive mornings (in conjunction with clearing the mammal trap lines). An additional afternoon search (c.2hr) was conducted at each sub-site. This search included observations of birds, reptiles and amphibians. Three dawn choruses (1hr) per trip were also conducted at each mountain. All incidental bird observations were also recorded. Due to the high mobility of birds and the relatively short distance between sub-sites the avifauna was not separated into the different sub-sites for each mountain.

Walking Transects

Night

Spotlighting transects of 1-1.5hr were conducted in each of the sub-sites on each mountain on both trips for mammals, birds, reptiles and amphibians. Two spotlights (30w) were used in each survey.

Day

Daylight walking transects of c. 2hr were con-

ducted each day (once at each sub-site) to search for birds and reptiles.

RESULTS

Mount Halifax had the highest diversity of birds (55 species) (Table 1) and ground-dwelling mammals (seven species) with Mount Cleveland having the greatest diversity of reptiles (18 species). Mount Elliot was notable in that it had the lowest observed diversity of all groups (Table 1).

The diversity of terrestrial vertebrates observed during these surveys is summarised in Table 1 and a complete species list with an index of relative abundance for each species (mammals and birds) is given in Appendix 1. Detailed mammal trapping results for each sub-site are included in Appendix 2.

MT CLEVELAND

There were considerable differences between the small mammal assemblages of each sub-site on the upper ridges of Mount Cleveland (appendix 2):

(1) The summit (site C1) and the rocky ridge (site C4) supported a small mammal assemblage consisting of *Dasyurus hallucatus, Melomys cervinipes, Isoodon macrourus*, and *Petrogale inornata*. Neither *D. hallucatus* or *P. inornata* were observed at the other sites. This is not surprising given the preference of these species for rocky habitat.

(2) Site C2 was dominated by *Melomys cervinipes*. Its density was very high at this site (20 individuals) with new individuals still being trapped after four days. The high density of *Xanthorrhoea* could be one of the factors contributing to the this because several individuals of *M. cervinipes* were observed nesting within the head of the grass trees and also eating the seeds. No *D. hallucatus* or *P. inornata* were observed in this habitat.

(3) The rainforest (site C3) contained fewer *Melomys cervinipes* in comparison to the other sites. This area may be more important during the dry season when water is not readily available in the drier areas.

Forty-three species of birds were observed on Mount Cleveland (Appendix 1). There was a much higher level of bird activity in, and on the edge, of the rainforest than elsewhere on the mountain. Generally the bird community was typical of the open forest of the Townsville region. However, due to the presence of the rainforest patch, there were also a number of closed forest species present (e.g. Scrub Turkey, Purple-crowned Pigeon, Wompoo Pigeon, Noisy Pitta, and Bower's Shrike-thrush).

MT HALIFAX

The summit area of Mount Halifax was found to have a mammal community typical of rainforest in this region (Appendix 1 and 2). The rainforest small mammal community was dominated by *Rattus fuscipes* and the small patches of heath vegetation were dominated by *Melomys cervinipes*.

There were several species which were expected but were not observed during the field surveys. These include the Red-legged Pademelon (*Thylogale stigmatica*), Brushtail Possum (*Trichosurus vulpecula*) and Green Ringtail (*Pseudochirops archeri*).

There were several small areas of heath that were of local significance (summit - grid ref. 339864 and near campsite - grid ref. 342862). The heath represented a very different habitat from the surrounding rainforest and, as such, significantly increased the habitat diversity of the area. Although the areas were probably too small to support vertebrates unique to that habitat, such as mammals and birds, there was a significantly different small mammal community present (compare sites H4 & H5 to sites H1, H2 & H3 in Appendix 2). It is also highly likely that these patches of heath would support restricted and endemic invertebrates (Graham, 1991). The heath contained concentrations of myrtaceous plant species such as *Leptospermum amboinense* and *Callistemon* sp., which could be an important seasonal food source for nectivorous birds and mammals.

MT ELLIOT

The results of the mammal trapping indicate that the Mount Elliot rainforest has a relatively depauperate small mammal community (Appendices 1 and 2). Only two species, *Rattus fuscipes* and *Melomys cervinipes* were trapped regularly and only in low numbers (Appendix 2). A single *Planigale maculata* was caught in an insect formalin trap. No sampling was conducted in the open forest; however this area was sampled by Lavery & Johnson (1974).

DISCUSSION

The three mountains examined differ considerably in topography and vegetation. These differences are reflected in relative abundances and species diversities of mammals and birds. Gra-

TABLE 1. Diversity of vertebrates by taxonomic group for Mount Cleveland, Mount Halifax and Mount Elliot

VERTEBRATE GROUP	MOUNT CLEVELAND	MOUNT HALIFAX	MOUNT ELLIOT
MAMMALS			
Families	6	4	3
Species	9	7	5
BIRDS			
Families	20	24	16
Species	43	55	31
REPTILES			
Families	8	6	5
Species	18	10	7
AMPHIBIANS			
Families	2	3	3
Species	5	5	4
TOTALS			
Families	36	37	27
Species	75	77	45

ham (1991) has previously discussed the survey of reptiles and amphibians from this expedition. Mount Halifax had the most diverse vertebrate fauna overall, as might be expected from its position, which is contiguous with other mountains and comparable habitats in the Paluma range. Small patches of heath near the summit of Mount Halifax may increase the habitat heterogeneity enough to produce endemic arthropods (Monteith, pers. comm.), but the areas are probably too small to have a significant effect on vertebrate communities. Both Mount Cleveland and Mount Elliot are discrete mountains in which it may be expected that diversities would be lower due to smaller, more isolated summit habitats. The relatively high diversity at Mount Cleveland is probably due to high habitat heterogeneity on the summit ridges.

Mount Cleveland is an important part of Bowling Green Bay national park as the habitat on and near the summit is unique within the park and is not well represented elsewhere in the region. The habitat on the upper ridges (*A. torulosa/Xanthorrhoea* forest ALTOR ET6M/X4S) is not widespread and contains a faunal community which is unusual (*Dasyurus hallucatus* and a high density of *Melomys cervinipes*). This community/habitat is therefore of significant importance to biological conservation both within this national park, and to the region. Patches of closed forest (e.g. site C3) are of great local significance as they greatly increase the diversity of habitats and the associated flora and fauna (as can be seen by the presence of a number of rainforest birds) although the much larger area of closed forest on nearby Mount Elliot is probably of greater regional significance.

The summit of Mount Elliot contains the largest block of rainforest within the Bowling Green national park and is regarded as being the southern limit of tropical rainforest proper (Winter & Atherton, 1987). The vertebrate fauna and flora surveys undertaken during this study also indicate that the rainforest on Mount Elliot has a high degree of affinity with the tropical rainforest to the north of Townsville. Taxa collected or noted by previous studies (Lavery 1968; Lavery & Johnson 1968; Lavery & Johnson 1974: Lavery & Seton, 1974) also indicate strong affinities with the rainforests along the Paluma Range to the north. There is one microhylid frog, *Cophixalus mcdonaldi,* endemic to the rainforest of Mount Elliot (Nix & Switzer, 1991; Zweifel, 1985). Very little is known about the biology of this very restricted species. *C. mcdonaldi* was calling during December and it appeared to be very common throughout the forest on the summit of Mount Elliot. Eight individuals were found during March by actively searching (three in rotted tree stumps, one in a crack between rocks, two under a flat rock and two sitting on a clutch of at least eight eggs inside a small (2cm diameter) hole in a solid rock face). Another interesting record was the capture of a *Planigale maculata* within rainforest when this species is usually considered to be an open forest species. It was unusual that no White-tailed Rats (*Uromys caudimaculatus*) were trapped or observed while spotlighting, since they have been recorded at Mount Elliot in the past, and are usually easy to trap and to spotlight.

Three species of birds recorded on Mount Elliot have not been recorded this far south before: Victoria's Riflebird, Bridled Honeyeater and Grey-headed Robin. These records increase the evidence of an affinity in the vertebrate fauna between the rainforest of Mount Elliot and tropical rainforest further to the north.

Mount Elliot is known to have a number of

endemic insect species, despite generally lower diversities than in the rainforests to the north (Graham, 1991). Mount Elliot is important in any biogeographical study of latitudinal trends in tropical biota, and greatly increases the local and regional biodiversity due to the inclusion of an area of tropical rainforest in an otherwise dry region.

Comments on Techniques

All sampling techniques have inherent biases that vary between taxa, seasons, habitats and weather conditions. Small mammals differ markedly in their relative trappability as illustrated by the capture of *Planigale maculata* in an insect formalin trap, which was not trapped in the small mammal traps. Pit traps (Mount Elliot, Mount Halifax) were found to be inefficient with respect to the effort required to install the pit lines. The pit traps were most useful in catching large ground dwelling invertebrates. Weather can have a large affect on observation biases with rain and/or mist making spotlighting and visual bird observations very difficult. Conversely, wet weather will increase the possibility of observing most amphibians and many reptiles. Most amphibians and reptiles are also less active during the winter months (dry season) making summer (wet season) sampling essential in tropical rainforests.

Habitat differences can have a drastic affect on the biases involved in most techniques. Dense vegetation makes visual observation of birds difficult and results in an increased importance of call identification. However, during these surveys it was found that, although most of the records were based on calls for the first two days, all bird species had been visually confirmed within five days. Dense vegetation also makes spotlighting for arboreal mammals very difficult, especially where there are no tracks or roads.

In summary, it is vital for vertebrate surveys to use as many different techniques as possible, and to sample during both wet and dry weather conditions to maximise the efficacy of the survey.

ACKNOWLEDGEMENTS

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APPENDIX 1

List of vertebrates observed during the fauna surveys of Mount Cleveland (Clv), Mount Halifax (Hal) and Mount Elliot (Ell). An index of abundance is given for mammals and birds for both the first and second field surveys (separated by a '/'). '-' — not observed, '0' — not observed on this trip, '1' — uncommon/only seen once or twice, '2' — common/observed regularly, '3' — abundant/observed several times on every census, '*' — observed at least once at this site during the course of both surveys. Species names follow Ingram & Raven (1991).

SPECIES	COMMON NAME	Clv	Hal	Ell
MAMMALS				
Dasyuridae				
Antechinus flavipes	Yellow-footed Antechinus	-	2/2	-
Antechinus stuartii	Brown Antechinus	-	1/1	-
Dasyurus hallucatus	Northern Quoll	2/0	-	-
Planigale maculata	Common Planigale	-	-	0/1
Peramelidae				
Isoodon macrourus	Northern Brown Bandicoot	2/2	-	-
Perameles nasuta	Long-nosed Bandicoot	-	1/1	-
Macropodidae				
Macropus agilis	Agile Wallaby	1/1	-	-
Petrogale inornata	Unadorned Rock Wallaby	1/1	-	-
Pteropidae				
Nyctimene robinsoni	Queensland Tube-nosed Bat	0/1	-	-
Pteropus alecto	Black Flying-fox	1/1	-	-
Syconycterus australis	Queensland Blossom-bat	1/0	-	-
Muridae				
Melomys cervinipes	Fawn-footed Melomys	3/3	3/3	2/2
Mus musculus	House Mouse	-	-	0/1
Rattus fuscipes	Bush Rat	-	3/3	3/2
Uromys caudimaculatus	White-tailed Rat	-	2/2	-
Suidae				
Sus scrofa	Feral Pig	1/1	2/2	2/2
BIRDS				
Casuariidae				
Casuaris casuaris	Southern Cassowary	-	1/1	-
Accipitridae				
Accipiter fasciatus	Brown Goshawk	-	0/1	-
Accipiter novaehollandiae	Grey Goshawk	1/0	-	-
Aquila audax	Wedge-tailed Eagle	1/1	0/1	0/1
Haliastur indus	Brahminy Kite	0/1	-	-
Falconidae				
Falco peregrinus	Peregrine Falcon	-	1/0	-
Megapodiidae				
Alectura lathami	Brush Turkey	1/1	2/2	2/1
Megapodius freycinet	Scrubfowl	-	1/0	1/0
Phasianidae				
Synoicus australis	Brown Quail	0/1	-	-
Columbidae				
Chalcophaps indica	Green-winged Pigeon	-	2/2	1/0
Columba leucomela	White-headed Pigeon	0/1	1/1	1/1
Geopelia humeralis	Bar-shouldered Dove	1/0	-	-
Lopholaimus antarcticus	Topknot Pigeon	-	1/0	1/0
Macropygia amboinensis	Brown Pigeon	-	2/1	2/1
Ptilinopus magnificus	Wompoo Pigeon	1/0	1/1	2/3
Ptilinopus regina	Red-crowned Pigeon	-	1/0	-
Ptilinopus superbus	Purple-crowned Pigeon	1/0	1/0	2/0
Loriidae				
Trichoglossus chlorolepidotus	Scaly-breasted Lorikeet	-	0/1	-
Cacatuidae				
Cacatua galerita	Sulphur-crested Cockatoo	1/1	2/2	0/1
Psittacidae				
Alisterus scalularis	King Parrot	-	1/1	-
Platycerus elegans	Crimson Rosella	-	2/3	-
Cuculidae				
Centropus phasianinus	Pheasant Coucal	3/3	-	-
Chyrsococcyx lucidus	Shining Bronze-Cuckoo	-	1/1	-
Cacomantis flabelliformis	Fantail Cuckoo	-	0/2	0/3
Tytonidae				
Tyto multipunctata	Lesser Sooty Owl	-	0/1	-
Strigidae				
Ninox boobook	Boobook Owl	1/1	-	1/0
Podargidae				
Podargus strigoides	Tawny Frogmouth	1/0	-	-
Aegothelidae				
Aegotheles cristatus	Australian Owlet Nightjar	1/0	—	
Apodidae				
Apus pacificus	Fork-tailed Swift	-	1/0	-
Alcedinidae				
Dacelo leachii	Blue-winged Kookaburra	0/1	-	-
Dacelo novaeguineae	Laughing Kookaburra	3/3	-	1/0
Meropidae				
Merops ornatus	Rainbow Bee-Eater	-	3/3	-
Pittidae				
Pitta versicolor	Noisy Pitta	-	3/3	3/0
Campephagidae				
Coracina lineata	Barred Cuckoo-Shrike	-	1/0	-
Coracina tenuirostris	Cicadabird	0/1	-	-
Lalage leucomela	Varied Triller	2/2	-	-
Orthonychidae				
Orthonyx spaldingii	Northern Logrunner	-	3/3	-
Psophodes olivaceus	Eastern Whipbird	-	3/3	-
Maluridae				

SPECIES	COMMON NAME	Clv	Hal	Ell
Malurus elegans	Red-backed Wren	1/0	-	-
Acanthizidae				
Oreoscopus gutturalis	Fernwren	-	1/1	-
Gerygone mouki	Brown Warbler	-	0/2	0/1
Gerygone palpebrosa	Fairy Warbler	2/2	0/1	-
Sericornis citreogularis	Yellow-throated Scrubwren	-	1/1-	
Sericornis frontalis	White-browed Scrubwren	-	2/0	3/3
Sericornis magnirostris	Large-billed Scrubwren	-	1/2	0/2
Monarchidae				
Monarcha melanopis	Black-faced Monarch	-	0/1	1/0
Monarcha trivirgatus	Spectacled Monarch	1/1	1/0	-
Myiagra cyanoleuca	Satin Flycatcher	1/0	-	-
Myiagra rubecula	Leaden Flycatcher	2/1	-	-
Rhipidura fuliginosa	Grey Fantail	-	3/3	1/1
Rhipidura rufifrons	Rufous Fantail	-	1/1	-
Eopsaltridae				
Heteromyias cinereifrons	Grey-headed Robin	-	3/3	3/3
Tregellasia capito	Pale-yellow Robin	-	3/3	2/3
Pachycephalidae				
Colluricincla boweri	Bowers Shrike-thrush	0/1	-	-
Colluricincla megarhyncha	Rufous Shrike-Thrush	3/3	1/11/1	
Pachycephala pectoralis	Golden Whistler	-	2/2	2/1
Pachycephala rufiventris	Rufous Whistler	-	1/0	-
Pachycephala simplex	Grey Whistler	-	1/0	1/0
Dicaeidae				
Dicaeum hirundinaceum	Mistletoebird	-	0/1	-
Meliphagidae				
Acanthorhynchus tenuirostris	Eastern Spinebill	-	2/3	1/0
Meliphaga chrysops	Yellow-faced Honeyeater	-	-	1/0
Meliphaga frenatus	Bridled Honeyeater	-	2/2	2/0
Melaphaga gracilis	Graceful Honeyeater	-	1/0	-
Melaphaga notata	Yellow-spotted Honeyeater	3/3	1/0	-
Melaphagi lewinii	Lewins Honeyeater	-	3/3	2/2
Melithreptus lunatus	White-naped Honeyeater	1/0	-	-
Myzomela obscura	Dusky Honeyeater	1/0	0/1	-
Philemon novaeguineae	Helmeted Friarbird	1/0	-	-
Philemon corniculatus	Noisy Friarbird	3/0	1/0	-
Phylidonyris nigra	White-cheeked Honeyeater	-	0/1	-
Estrildidae				
Neochmia temporalis	Red-browed Firetail	1/0	-	-
Dicruridae				
Dicrurus bracteatus	Spangled Drongo	1/0	-	-
Cracticidae				
Strepera graculina	Pied Currawong	2/3	0/3	3/2
Ptilonorhynchidae				
Ailuroedus melanotis	Spotted Catbird	-	3/3	-
Scenopoeetes dentirostris	Toothbill Bowerbird	-	3/2	3/3
Paradisaeidae				
Ptiloris victoriae	Victoria's Riflebird	-	1/1	1/0

SPECIES	COMMON NAME	Clv	Hal	Ell
Corvidae				
Corvus orru	Australian Crow	2/0	-	-
REPTILES				
Gekkonidae				
Gehyra dubia		*	-	*
Heteronotia binoei	Bynoe's Gecko	*	-	-
Oedura ocellata		*	-	-
Oedura rhombifer		*	-	-
Pygopodidae				
Lialis burtonis	Burton's Legless Lizard	*	-	-
Scincidae				
Carlia pectoralis		*	-	-
Carlia rhomboidalis		*	-	-
Carlia rubrigularis		-	*	-
Carlia schmeltzii		*	-	-
Cyclodomorphus gerrardii		-	-	*
Egernia frerei		*	-	-
Sphenomorphus quoyii	Water Skink	-	*	-
Lampropholis basiliscus		-	*	*
Lampropholis coggeri		-	*	-
Lampropholis mirabilis		-	-	*
Sphenomorphus punctulatus		*	-	-
Agamidae				
Diporiphora australis	Two-line Dragon	*	-	-
Physignathus lesueurii	Water Dragon	-	*	-
Varanidae				
Varanus scalaris	Spotted Tree-monitor	*	*	-
Varanus varius	Lace Monitor	-	-	*
Boidae				
Morelia amethistina	Amethystine Python	-	*	-
Morelia maculosa	Childrens Python	*	-	-
Morelia spilota	Carpet Python	*	-	*
Colubridae				
Dendrelaphis punctulata	Common Tree Snake	*	*	-
Elapidae				
Acanthophis antarcticus	Death Adder	-	-	*
Demansia vestigiata	Black Whipsnake	*	-	-
Demansia psammophis	Yellow-faced Whipsnake	-	-	*
Demansia torquata	Collared Whipsnake	*	-	-
Pseudechis porphyriacus	Red-bellied Black Snake	-	*	-
Pseudonaja textilis	Eastern Brown Snake	*	-	-
Rhinoplocephalus nigrescens	Smalleyed Snake	-	*	-
AMPHIBIANS				
Bufonidae				
Bufo marinus	Cane Toad	*	*	*
Hylidae				
Litoria caerulea	Green Tree Frog	*	-	-
Litoria fallax		*	-	-
Litoria gracilenta		*	-	-

SPECIES	COMMON NAME	Clv	Hal	Ell
Litoria leuseuri	Stony-creek Frog	-	*	*
Litoria nannotis	Torrent Tree Frog	-	*	-
Litoria rothii	Red-eyed Tree Frog	*	-	-
Microhylidae				
Cophixalus mcdonaldi		-	-	*
Cophixalus ornatus		-	*	-
Sphenophryne robusta		-	*	-

APPENDIX 2

Results of small mammal trapping at each sub-site on Mount Cleveland, Mount Halifax and Mount Elliot. Data are the number of individuals caught per hundred trap nights at each trapping site. The results of each field trip (TRIP) are given separately.

MOUNT CLEVELAND					
SPECIES	TRIP	C1	C2	C3	C4
Dasyurus hallucatus	1	2.0	—	—	1.0
	2	—	—	—	—
Isoodon macrourus	1	2.0	2.0	1.0	2.0
	2	1.0	2.0	1.0	1.0
Melomys cervinipes	1	9.0	20.0	2.0	10.0
	2	19.0	23.0	6.0	21.0

MOUNT ELLIOT					
SPECIES	TRIP	E1	E2	E3	E4
Melomys cervinipes	1	1.1	3.2	2.2	—
	2	2.0	1.0	—	1.0
Mus musculus	1	—	—	—	—
	2	2.0	—	—	—
Planigale maculata	1	—	—	—	—
	2	—	—	1.0	—
Rattus fuscipes	1	4.3	2.2	4.3	5.4
	2	—	4.0	1.0	—

MOUNT HALIFAX						
SPECIES	TRIP	H1	H2	H3	H4	H5
Antechinus flavipes	1	3.8	—	2.5	2.5	—
	2	4.2	—	—	—	—
Antechinus stuartii	1	—	—	2.5	—	—
	2	2.1	—	—	—	—
Melomys cervinipes	1	1.3	—	—	5.0	10.0
	2	2.1	—	—	4.2	—
Rattus fuscipes	1	12.5	13.8	20.0	22.5	2.5
	2	16.7	14.6	18.8	8.3	29.2
Uromys caudimaculatus	1	2.5	1.3	1.3	—	—
	2	2.1	2.1	4.2	—	—

PREFACE

The preparation for this International Congress was superbly managed by two Organising Committees. All members worked very hard and I am very grateful for their cooperation. The Western Australian Museum was the centre of the Scientific and Publications Committee of Dr Mark S. Harvey, Dr Bill F. Humphreys, and Dr Barbara York Main. This group, lead by Mark Harvey, formed a fine team who very capably managed all scientific and publication matters from manuscript submission to acceptance through the Congress program and photographic awards.

The local Organising Committee included Dr Valerie Davies (Secretary), and Ms Tracey Churchill, Ms Jan Green, Ms Judy Grimshaw, Mr Phil Lawless and myself. That group managed diverse aspects of Congress organisation. Mr David Nebauer assisted committee members during the registration process. My preparation was initially assisted by Ms Julie Gallon. In July 1991, Mr Philip Lawless took up the reins from Julie and proved to be a very dedicated and astute lieutenant. Emeritus Professor George Davies assisted the Secretary throughout the entire Congress period.

Delegates from Russia, Kazakhstan, The People's Republic of China, Madagascar, Mexico, Hungary, India, Belgium, North America, Germany, and Namibia were provided with varying degrees of sponsorship by the Queensland Museum Board of Trustees and sponsors. Their travel arrangements, often highly complex and problem-rich, were very capably managed by Ms Joanne Lavelle, then of State of Corporate Travel. Many a Congress delegate will no doubt fondly remember the Committee reception at the International airport. Several appreciated the kind hospitality of Mr Tony Luck, Microrim (Australia), of Camira, in an 'Aussie barbeque' before the Congress.

Organisation of the Post-Congress tour to Cape Tribulation, was greatly facilitated by the much appreciated contributions of Ms Linda Stanley, Ms Esther Cullen, and Cliff and Gail Truelove.

Editorial assistance was provided by Ms Gudrun Sarnes, Philip Lawless and Mr Neale Hall.

The Congress organisers very gratefully acknowledge the financial donations of Australian Geographic Magazine, Western Australian Museum, Amalgamated Pest Control, Australian Museum, Museum of Victoria, South Australian Museum, Commonwealth Bank, University of Queensland–Entomology & Zoology Departments, Griffith University–School of Australian Environmental Sciences, QANTAS Airlines, Australasian Arachnological Society, CSIRO, Division of Entomology, and the British Council. Financial support was also received from International Conference Support (loan) and the Australian Tourist Commission. The Queensland Museum Board of Trustees provided generous support for the Congress and the publication of these proceedings.

Robert J. Raven
Chairman, XIIth International Congress of Arachnology

October 11, 1993

Chairman: Dr Robert Raven.

39 Dr Joachim Adis
88 Ms Rachel Allan
70 Dr Andrew Austin
26 Dr Léon Baert
10 Mr Alberto Barrion
18 Dr Timothy Benton
73 Ms Emily Bolitho
24 Dr Allen Brady
3 Ms Cathy Car
95 Dr James Carico
81 Mr Kefyn Catley
74 Ms Tracey Churchill
79 Dr Jon: Coddington
89 Dr Valerie Davies
112 Prof. George Davies
97 Dr Christa Deeleman
8 Dr Eric Duffey
7 Mrs Rita Duffey
23 Dr William Eberhard
41 Dr Janet Edmunds

80 Prof. Malcolm Edmunds
17 Dr Mark Elgar
72 Mr Theodore Evans
19 Dr Peter Fairweather
44 Mr Richard Faulder
84 Dr Martin Filmer
29 Dr Lyn Forster
56 Dr Ray Forster
48 Dr Rosemary Gillespie
12 Ms Maureen Glover
96 Dr Michael Gray
38 Ms Jan Green
122 Ms Judy Grimshaw
82 Dr Charles Griswold
6 Dr Cristina Guerrero-Trejo
62 Ms Grace Hall
109 Ms Myriam Haquin
71 Dr Mark Harvey
87 Dr Johannes Henschel
63 Mr David Hirst

86 Dr Hubert Höfer
47 Mr Chris Holden
110 Dr Peter Horak
99 Dr Gustavo Hormiga
33 Dr Peter Hudson
118 Dr Bill Humphreys
117 Dr Glenn Hunt
58 Ms Heli Hurme
64 Dr Robert Jackson
28 Dr Rudy Jocqué
14 Ms Sarah Kariko
2 Mr Joseph Koh
69 Dr Akio Kondo
101 Dr Peter Koomen
60 Dr Seppo Koponen
59 Ms Salla Koponen
50 Prof. Otto Kraus
51 Dr Margarete Kraus
113 Dr Christian Kropf
76 Mr Philip Lawless

45 Dr Pekka Lehtinen
52 Mr Peter Linklater
49 Dr Adam Locket
21 Mr Alan Longbottom
32 Mr Roger Lowe
42 Dr Volker Mahnert
30 Prof. A.R.(Bert) Main
43 Dr Barbara York Main
106 Dr Patrick Marc
105 Ms Sylvie Marc-Mallet
75 Mr Roland Mckay
57 Mr Graham Milledge
121 Dr Gary Miller
107 Mrs Patricia Miller
91 William Miller
98 Dr Monika Müller
31 Mr John Murphy
9 Mrs Frances Murphy
67 Dr Hirotsugu Ono
61 Dr Vladimir Ovtsharenko

11 Dr S. Palanichamy
119 Dr Ralph Platen
78 Prof. Norman Platnick
83 Dr Gary Polis
35 Dr Simon Pollard
22 Dr William Preston
114 Dr Robert Raven
120 Dr George Roderick
27 Dr Christine Rollard
34 Dr Jerome Rovner
16 Mrs Phyllis Rovner
77 Mr Ferenc Samu
68 Dr Peter Schwendinger
90 Dr Paul Selden
108 Dr Gail Stratton
25 Dr Keith Sunderland
92 Ms Katherine Suter
93 Mrs Valerie Suter
94 Dr Robert Suter
53 Dr Hirohumi Suzuki

15 Dr John Talent
115 Dr Koichi Tanaka
111 Dr Chingis Tarabaev
66 Mr Phil Taylor
40 Ms Margaret Tio
116 Dr Nobuo Tsurusaki
46 Dr Gabriele Uhl
5 Dr Ignacio Vazquez
13 Dr Lenny Vincent
55 Mr Cor Vink
54 Dr Fritz Vollrath
4 Ms Julianne Waldock
85 Mr Doug Wallace
1 Dr Friedrich Wallenstein
65 Dr Mary Whitehouse
37 Mr Graham Wishart
36 Mrs Gwen Wishart
100 Dr Jorg Wunderlich
104 Dr Frederic Ysnel

From the President's Desk

The XII International Congress of Arachnology was held at the Queensland Museum, Brisbane, from 12th to 18th July, 1992 under the joint auspices of the Trustees of the Queensland Museum and the Centre International de Documentation Arachnologique. More than 122 registrants from 32 countries and 37 accompanying persons participated.

The 114 presented papers covered nearly all fields of arachnological research, reflecting the progress in our knowledge of arachnids. This progress may encounter some scepticism from particularly the older, loyal participants since every president in each presidential report underlines the 'progress made during the last three years'. A congress program does not reflect the actual research level, but only the fields of interests of participants whose attendance at congress depends on economic or other factors. Real progress can be emphasised in the fields of biology, ecology, bio-indication and phylogeny. However, we might be regressing in taxonomy because the number of taxonomists remains stable while the numbers of identifications requested by ecological and other studies (raising new taxonomical problems) are increasing. Some arachnid groups will perhaps be 'orphaned' in the near future as specialists retire from active study.

Arachnids are fascinating animals of great biological importance. Is there any reason not to tell this more frequently to 'the public'? Ecologists should allow a reasonable fee for identification of their material when submitting grant applications.

At the meeting of CIDA members held during the Congress, Dr R. Jocqué was elected the new CIDA president.

The congress excursion was held mid-week at O'Reilly's, Lamington Plateau, where participants could discover the rich bird and arthropod fauna of the forest, stroll through the botanical garden or have an exciting canopy walk.

Brisbane was a marvellous occasion to meet friends and colleagues, but also (at least for me) a wonderful time to discover a fascinating continent and its plants and animals, and I am sure that we will come again. Thanks to all of the organising staff and the people we had the chance to meet for their friendliness and helpfulness.

'Le Roi est mort, vive le Roi'. Hopefully we will meet in Geneva in 1995.

Volker Mahnert

President, Centre International de Documentation Arachnologique 1989-1992

FOSSIL ARACHNIDS–RECENT ADVANCES AND FUTURE PROSPECTS

PAUL A. SELDEN

Selden, P.A. 1993 11 11: Fossil arachnids–recent advances and future prospects. *Memoirs of the Queensland Museum* **33**(2): 389-400. Brisbane. ISSN 0079-8835.

Until 5 years ago, the arachnid fossil record was sparse. It was dominated by a comparative wealth of forms in Carboniferous Coal Measure sediments, and near-modern forms from Palaeogene Baltic amber. Both these relatively well-documented sources and the few reported finds elsewhere in the record suffered from erroneous interpretations. In recent years, new interpretations of existing fossils and a few spectacular new finds have filled in the gaps in the record and changed our knowledge and views of the course of arachnid evolution. Particular examples are: Devonian pseudoscorpions and spiders, book-lungs in Carboniferous scorpions, Triassic mygalomorph spiders, and Jurassic and Cretaceous araneomorph spiders. Phylogenetic systematic analyses of extant arachnids have produced evolutionary scenarios which conflict with the observed fossil record in parts. The newly expanded knowledge of the fossil record allows better tests for the cladograms. Future work on reinterpretation of known Carboniferous and Palaeogene fossils, on rare Mesozoic arachnids, and on arachnids in the earliest known terrestrial ecosystems in the Silurian will add to our knowledge of the fossil record of the arachnids and further enhance testing of phylogenetic hypotheses.□*Aglaspidida, Arachnida, Chelicerata, palaeontology, phylogeny, Pycnogonida.*

Paul A. Selden, Department of Geology, University of Manchester, Manchester M13 9PL, United Kingdom; *10 November, 1992.*

For most of this century, one name dominated the literature on fossil arachnids, that of Alexander Petrunkevitch (1875-1964). Petrunkevitch (1955; in Størmer, 1955) summarized the arachnid fossil record to mid-century (Fig. 1) in the 'Treatise on Invertebrate palaeontology' and although he published on amber spiders after 1955, the broad view of the fossil record of chelicerates remained little changed until about a decade ago. Few workers either published on fossil arachnids or disputed Petrunkevitch's assignments during his lifetime. Only recently, during restudy of the fossils, have many errors and misinterpretations in his work come to light.

In the fossil chelicerate record published in the 'Treatise' (Fig. 1), the Merostomata (essentially aquatic chelicerates) are separated from the Arachnida. Second, most of the arachnid side consists of dashed lines converging towards the base of the Cambrian, indicating lack of fossil record and uncertainty of affinities respectively. Third, apart from one dubious palpigrade and some scorpions, there are no other records of Mesozoic (Triassic-Cretaceous) arachnids. Fourth, there is a clear pattern in the temporal distribution of the fossils: a concentration of records in the Upper Carboniferous, and many modern groups also occur in the Palaeogene (early Tertiary). The former records are from the Coal Measures of Europe and North America, for example: Mazon Creek, Illinois; Coseley, England; and Nyrany, Czechoslovakia. The Palaeogene occurrences are mainly from Baltic amber. Although Trigonotarbida and a questionable record of Araneae had been known from the Devonian Rhynie Chert of Scotland since Hirst (1923), they were omitted from the diagram. (In addition, Petrunkevitch knew of undescribed Lebanese amber opilionids and some Cretaceous spiders from Manitoban amber).

Petrunkevitch developed theories on the evolution of arachnids, which resulted in his superordinal classifications of 1945 and 1949. He recognized a number of 'evolutionary trends', such as the movement of the mouth rearwards from the Xiphosura to the arachnids, and the reduction of the metasoma to a tail or pygidium. One of the most important characters used in his classifications is the width of the connection between prosoma and opisthosoma, i.e. reduction of the first abdominal somite to a pedicel. Petrunkevitch (1945) divided the class Arachnida into two subclasses, Latigastra and Caulogastra, on the basis of a broad or a narrow prosoma-opisthosoma connection respectively. Later, Petrunkevitch (1949) added the subclass Soluta to the scheme to include solely his new order Trigonotarbida which he considered exhibit both wide and narrow junctions. Another subclass, the

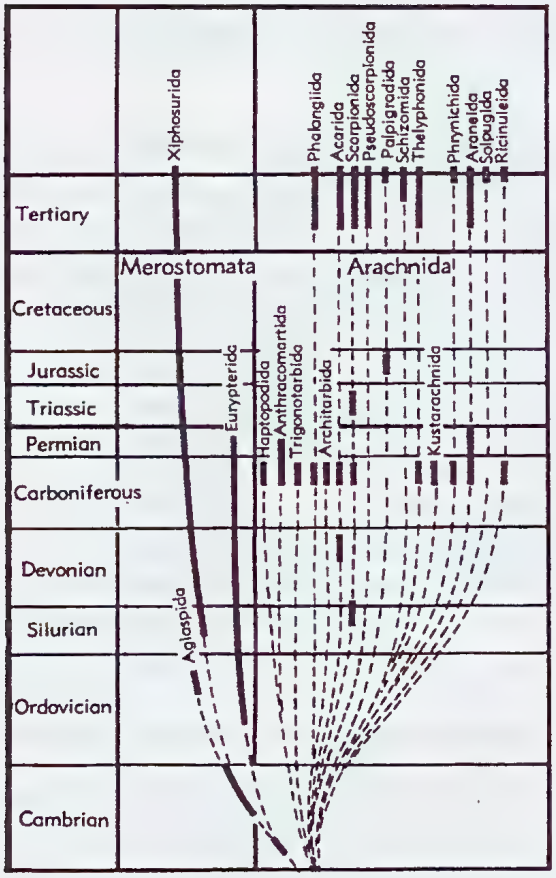


FIG. 1. Stratigraphic ranges of Chelicerata and Aglaspidida and presumed phylogenetic relationships (from Størmer, 1955).

Stethostomata, was created at this time to accommodate the orders Anthracomartida and Haptopoda which supposedly have a broad prosoma-opisthosoma junction and a unique coxosternal region. Petrunkevitch's (1949) classification scheme, used in the 'Treatise', has not stood the test of time. Weygoldt and Paulus (1979) noted its use in some textbooks but pointed out severe deficiencies in the scheme when other characters are taken into account.

Petrunkevitch was a devout proponent of the idea of the 'decoupling' of macroevolution and microevolution. He envisaged major features (those which define higher taxa) originating by mutation or other accelerated evolution, whereas minor morphological differences (those which separate species, for example) could provide only long, slow evolution and rarely produced higher taxa (Petrunkevitch, 1952, 1953). Petrunkevitch (1955) envisaged extinction occurring when irreversible evolutionary trends took groups down blind alleys–useful trends which proved lethal when taken to extreme or when environmental conditions changed. Characters could therefore be described as 'major' or 'minor', depending on the taxonomic rank they diagnose. Provided the 'rank' of a character is not decided *a priori*, there is no problem; however, difficulties arise when character states do not clearly change at taxon boundaries. For example, in a diagnosis of the subclass Soluta Petrunkevitch, 1949 is: 'abdomen composed of 8 to 11 segments' (Petrunkevitch, 1955, p. P107). Petrunkevitch described this variability as the character being in a 'labile' state. So, the subclass Soluta is diagnosed on the *labile condition* of the abdominal segmentation, the presence of *either* a broad *or* a narrow junction between the opisthosoma and prosoma (see above), and the *overall resemblance* of the coxosternal region to that in spiders [my italics]. Petrunkevitch (1955) argued that solutes are not spiders because of the combination of characters in the group, and additionally they showed a single series of marginal plates on the opisthosoma. Obviously, such a group could also be considered a collection of quite different animals placed together through their shared possession of a spider-like coxosternal region.

Restudy of fossil solutes reveals that the problem lies mainly in Petrunkevitch's inability to correctly interpret fossil material. The number of segments in the Soluta is invariably 11 (Shear *et al.*, 1987) but the number Petrunkevitch interpreted in each specimen differed according to its preservation. Thus, where a 2-segmented pygidium was preserved, then 2 additional segments were counted over specimens which did not preserve this organ, and the short first abdominal segment is not always visible in fossils. Similarly, the interpretation of the prosoma-opisthosoma junction depended on how closely these tagmata were conjoined in the fossil.

Petrunkevitch described *Trigonomartus pustulatus*, and noted (1913, p. 104): 'The cephalothorax being much harder, kept more or less its shape, and what appears on it as a median crest was in reality a median groove. The irregular, polygonal depressions were evidently thickened areas of the chitin and formed in life low elevations.' But, two pages before he had diagnosed the new genus thus: 'Carapace triangular with a median crest in the posterior half, covered with irregular polygonal depressions.' Thus he had recognized that the fossils were

external moulds but diagnosed the genus as if they were casts. The error perpetuated until 1955 when, in the 'Treatise' (p. P112), the diagnosis became 'Carapace triangular, high, with median crest and a pustulose surface, without eyes. Abdomen with pustulose surface' Thus, pustules were recognized but the median crest remained, without explanation for the emendation. Furthermore, eyes exist in *Trigonomartus* (Petrunkevitch, 1913, pl. 9, fig. 49, in the same place as in *Aphantomartus* (Pocock 1911, Pl. II, fig. 6). These two genera were synonymized by Selden and Romano (1983). As well as misinterpreting fossils, Petrunkevitch produced some illogical taxonomic arguments. In 1945, he erected the Aphantomartidae for eophrynids with 7 abdominal tergites (i.e. *Aphantomartus areolatus* Pocock, 1911). In 1949, he erected the Trigonomartidae, and, recognizing that *Aphantomartus* had 8 abdominal tergites, not 7, he stated (p. 256): 'This means that the Family Aphantomartidae becomes a synonym of Trigonomartidae, the number of abdominal segments having served as the only character of distinction.' Why not place the contents of the new 'Trigonomartidae' in the existing Aphantomartidae? Aphantomartidae has priority and was redefined by Selden and Romano (1983). Furthermore, illustrations purporting to differentiate *Aphantomartus* and *Trigonomartus* (Petrunkevitch 1955, figs 80, 1 and 3) are unrepresentative and merely emphasise different characters of the same genus. Fig. 80, 3 is not *Aphantomartus areolatus*, as stated in the text, but a copy from Pruvost (1919, fig. 42) of *A. pococki*, with eyes drawn on incorrectly!

Consider also the Phalangiotarbida. Kjellesvig-Waering redescribed this group just before his death in 1979, and the MS was being prepared for posthumous publication (see Kjellesvig-Waering, 1978). In the MS, Kjellesvig-Waering, a renowned taxonomic 'splitter', reduced Petrunkevitch's 10 genera and 13 species to four genera and five species. He stated in the introduction to his MS: 'Seldom, if ever, has a fossil group with such uncomplicated, mostly easily determinable morphological characters, been subjected to such misunderstanding and careless and erroneous work as has the order Phalangiotarbida Haase, 1890. The main reason for this state has been the complete failure of some of the workers in this group to understand fundamental paleontological principles of preservation, for example, molds and casts, external and internal, along with results of compaction and consequent reflection or impression of ventral into dorsal surfaces and vice versa.' Kjellesvig-Waering's conclusions on functional morphology and phylogeny, both in this MS and his other work, are not without dispute, but his long experience with the taxonomy of fossil chelicerates was generally reliable. Kjellesvig-Waering wrote in his MS: 'The question of whether Phalangiotarbida Haase, 1890, or Architarbida Petrunkevitch, 1945 is the proper name for this order of arachnids has not been settled, although it is difficult to understand why any question should have arisen in the first place.' What Petrunkevitch did was to substitute an existing name with one based on better preserved specimens of the order: 'What is more reasonable than to regard the Family Architarbidae as the most characteristic one of the Order and to emphasize this fact by using a proper derivative of the generic name for the Order?' (Petrunkevitch, 1945, p. 11).

The above examples show that much work is needed on fossil arachnids already in collections, in addition to study of the many new fossils awaiting description.

THE FOSSIL RECORD
(Fig. 2)

Arachnid Relatives

The extinct aglaspidids are probably not chelicerates since they bear neither chelicerae nor other features which would ally them with the Chelicerata over any other arthropod group (Briggs *et al.*, 1979). The fossil record does not help to determine the systematic position of the enigmatic pycnogonids. Chelicerae are not a prerequisite for a chelicerate. *Sanctacaris* Briggs and Collins, 1988 from the Middle Cambrian Burgess Shale of British Columbia lacks chelicerae but was included in the phylum because of a combination of characters unique to Chelicerata: six pairs of prosomal appendages, cardiac lobe, prosoma and opisthosoma, and anus at rear of last trunk segment. *Sanctacaris* was described as sister to all other chelicerates, but may not be the oldest chelicerate because a dubious xiphosuran carapace of Lower Cambrian age, *Eolimulus alatus* (Moberg, 1892) was recorded from Öland, Sweden. Xiphosura are the most primitive chelicerates in existence and, though previously allied with the Eurypterida in the Merostomata, most authors place Xiphosura with either the Scorpionida (Bergström, 1979, 1981; Bergström *et al.*, 1980; van der Hammen, 1985, 1986) or as sister to all other chelicerates (except

Sanctacaris) (Grasshoff, 1978; Boudreaux, 1979; Paulus, 1979; Weygoldt and Paulus, 1979; Weygoldt, 1980), thereby rendering Merostomata an unnatural group.

Scorpions

Scorpions are the arachnid group with the earliest known ancestors; the most ancient known scorpion is *Dolichophonus loudonensis* (Laurie, 1889) from the Llandovery of the Pentland Hills, near Edinburgh, Scotland. Kjellesvig-Waering (1986) proposed a controversial classification scheme. Stockwell (1989) produced a more acceptable classification scheme of Scorpionida which included fossils, but it has yet to be published formally. A linchpin of Kjellesvig-Waering's classification was the supposed Devonian gilled scorpion described as *Tiphoscorpio hueberi*. Restudy of this material (Selden and Shear, 1992) revealed that it is not a scorpion but an arthropleurid myriapod!

The early Silurian record of scorpions could be interpreted as representing the earliest terrestrial animals since all modern scorpions are terrestrial. However, all Silurian fossil scorpions occur in marine or marginal marine sediments, and morphological features suggest an aquatic mode of life. Petrunkevitch (e.g. 1953) considered all fossil scorpions were terrestrial, but other workers (e.g. Wills, 1947; Stormer, 1970; Rolfe and Beckett, 1984; Kjellesvig-Waering, 1986) argued for an aquatic habitat for Silurian scorpions at least. Evidence for aquatism among fossil scorpions are: gills and digitigrade tarsi, as well as the absence of terrestrial modifications such as coxal apophyses, stigmata, book lungs, trichobothria, highly developed pectines and plantigrade tarsi. There is overlap in the ranges of aquatic and terrestrial scorpions but the first terrestrial forms probably appeared the Devonian (Selden and Jeram, 1989). It is not easy to decide whether a given fossil had an aquatic or terrestrial mode of life; the original environment of the enclosing sediment is commonly the best clue, but a recent find is worthy of especial note: well preserved book lungs in a Carboniferous (Visean) scorpion from East Kirkton, near Edinburgh, Scotland (Jeram, 1990). Few new records of fossil scorpions have turned up in recent years although in the otherwise sparsely recorded Mesozoic, scorpions reported from the Triassic of France (Gall, 1971), and the Cretaceous of Brazil (Campos, 1986) are currently under study.

Pseudoscorpionida

Many pseudoscorpions are known from the Tertiary (mainly in ambers, e.g. listed in Schawaller (1982, table 1), and some are known from Cretaceous ambers of Lebanon (Whalley, 1980) and Manitoba (Schawaller, 1991). However, the most important fossil pseudoscorpions are well preserved specimens of *Dracochela deprehendor* (Shear *et al.*, 1989; Schawaller *et al.*, 1991), in the Upper Devonian mudstones of Gilboa, New York. Only protonymph and tritonymph are known which, though modern in many aspects, cannot be assigned with confidence to extant taxa because both diagnostic characters in the fossils and cladistic assessment of extant forms are lacking.

Solifugae

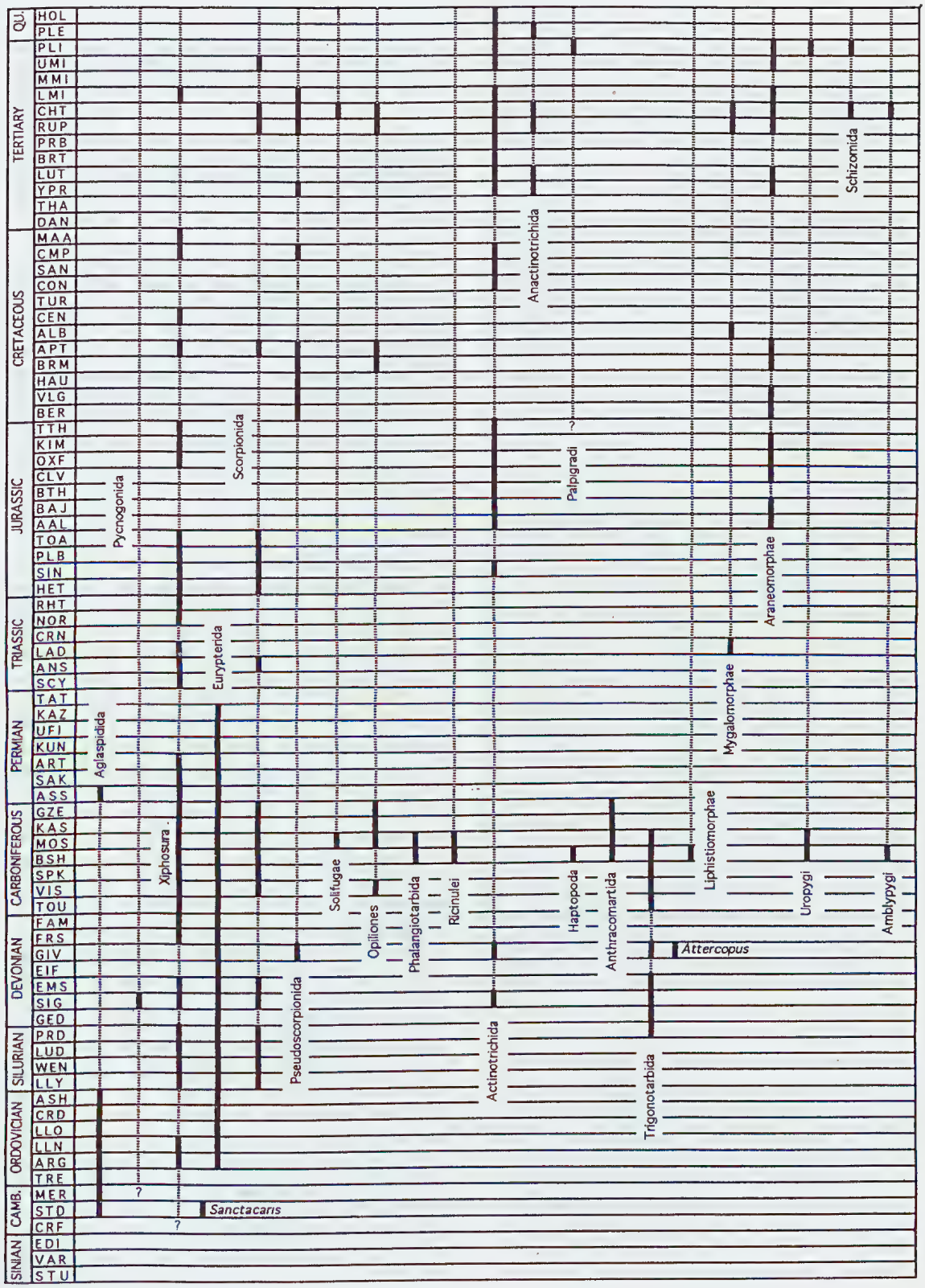
The Carboniferous solifuge, *Protosolpuga carbonaria* Petrunkevitch, 1913, was described as being in a very poor state of preservation. It is impossible to judge the validity of the identification from the published photograph and drawing. The only reliable fossil solifuge is *Happlodontus proterus* Poinar and Santiago-Blay, 1989, from Oligocene Dominican amber.

Opiliones

Until recently, Opiliones had a fairly typical arachnid fossil record, being known only from Upper Carboniferous strata and Tertiary ambers. In 1985 a specimen was discovered in Lower Carboniferous rocks of East Kirkton, near Edinburgh, Scotland (Wood *et al.*, 1985), and a year later, one was described from the Lower Cretaceous of Koonwarra, Victoria, Australia (Jell and Duncan, 1986). Both of these unnamed specimens are long-legged opilionids but no further identification is possible (pers. obs.).

The order Kustarachnida Petrunkevitch, 1913 is included with the Opiliones, following Beall (1986).

FIG. 2. Current knowledge of the fossil record of Aglaspidida, Pycnogonida and Chelicerata; data in Selden (1993). Solid lines denote actual occurrence in the stage(s) concerned; interrupted lines indicate presumed occurrence in intervening stages. ? denotes doubtful record. Note that taxon ranks are not equivalent; occurrences of important genera *Sanctacaris* (most plesiomorphic chelicerate) and *Attercopus* (oldest and most plesiomorphic spider) are shown separately. Stratigraphic resolution is to stage; abbreviations in second column refer to standard stage names (see e.g. endpapers of Briggs and Crowther, 1990).


QU.
TERTIARY
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CARBONIFEROUS
DEVONIAN
SILURIAN
ORDOVICIAN
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STU
Aglaspidida
Pycnogonida
Xiphosura
Eurypterida
Scorpionida
Palpigradi
Anactinotrichida
Schizomida
Araneomorphae
Mygalomorphae
Liphistiomorphae
Uropygi
Amblypygi
Haptopoda
Anthracomartida
Trigonotarbida
Actinotrichida
Pseudoscorpionida
Opiliones
Solifugae
Phalangiotarbida
Ricinulei
Attercopus
Sanctacaris
?
?

Phalangiotarbida

The situation of the phalangiotarbids has been described above. This group is only known from the Upper Carboniferous but fossils are widespread in European and North American coalfields.

Ricinulei

Ricinulei are known only from the Upper Carboniferous of Europe and North America, and the New and Old World tropics at the present day (their range extends outside the tropics mainly by cavernicole species). A recent revision of the fossils (Selden, 1992) revealed a greater diversity in the Carboniferous than today, but based on an essentially similar body plan. It appears that the group has remained in warm, humid habitats (equatorial forest litter and caves) throughout its geological history.

Mites

The oldest mites are Actinedida (Prostigmata) from the Lower Devonian Rhynie Chert of Scotland (Hirst, 1923). Other Devonian Actinotrichida are known from Gilboa, New York (Norton *et al.*, 1988, 1989; Kethley *et al.*, 1989). A few Jurassic and Cretaceous Actinotrichida are known (e.g. Bulanova-Zakhavatkina, 1974; Krivolutsky and Ryabinin, 1976; Sivhed and Wallwork, 1978), but the majority of fossil mites are oribatids from Baltic amber (e.g. Koch and Berendt, 1854; Sellnick, 1918, 1931). Anactinotrichida are very poorly represented in the fossil record; there are no fossil Opilioacarida or Holothyrida and only a few, somewhat suspect, records of Ixodida (e.g. Scudder, 1890) and Gamasida (e.g. Hirschmann, 1971). Fossil mites are probably found routinely in palynological preparations but are unreported. With the growth of micropalaeontological techniques in the study of fossil arthropods it is likely that many more fossil mites will be identified.

Palpigradi

The preservation potential of palpigrades is even lower than that of mites. Their small size, thin cuticles and interstitial habitats makes them difficult objects of study when Recent or fossil. *Sternarthron zitteli* Haase, 1890, from the Jurassic lithographic limestone of Solnhofen, Germany, is doubtful; the only good fossil palpigrade is *Palaeokoenenia mordax* Rowland and Sissom, 1980, from the 'Onyx Marble' quarries (Pliocene) of Arizona.

Haptopoda

This monotypic order was established by Pocock (1911) on the basis of the subdivided tarsus of the first leg. Petrunkevitch (1949) cleaned and reexamined the specimens, and redefined the order based on a new interpretation of the abdominal segmentation. The group would repay restudy along with Anthracomartida and Trigonotarbida.

Anthracomartida

Together with Haptopoda, this order forms Petrunkevitch's 1949 subclass Stethostomata. In a discussion of the rationale for separating Stethostomata from Soluta (Shear and Selden, 1986; Shear *et al.*, 1987), it was concluded that the only feature separating anthracomartids from trigonotarbids is two versus one rows of marginal tergal plates on the opisthosoma. Again, this common Upper Carboniferous group needs careful restudy.

Trigonotarbida

Trigonotarbids are the best known extinct arachnid group on account of their excellent preservation in the Devonian Rhynie Chert of Scotland and Gilboa mudstones of New York and are among the first known land animals (Jeram *et al.*, 1990). First described from Upper Carboniferous rocks (Buckland, 1837; Fritsch, 1901; Pocock, 1902, 1903, 1911), Hirst (1923) described the first Devonian specimens (from Rhynie), and Størmer (1970) described forms from the Middle Devonian of Alken-an-der-Mosel, Germany. Trigonotarbida is one of the few arachnids groups found relatively frequently in Palaeozoic terrestrial rocks of from Argentina (Pinto and Hünicken, 1980), Spain (Selden and Romano, 1983), Czechoslovakia (Opluštil, 1985), and Germany (Jux, 1982).

The exquisite preservation of the Rhynie Chert meant that Hirst (1923) could describe minute details of the trigonotarbids from that deposit. Trigonotarbids from Gilboa (Shear *et al.*, 1987) not only confirmed Hirst's observations but also uncovered further morphological features of these interesting animals. Later work has shown that some of the species described as trigonotarbids in 1987 were really spiders or other pulmonate arachnids (Selden *et al.*, 1991), but the systematic position of the Trigonotarbida, sister to all other pulmonates, was strengthened. A trigonotarbid and centipedes, found together with early land plants in Silurian (basal Přídoli) sediments at Ludford Lane, Ludlow, England (Jeram

et al., 1990), pushed back the earliest record of land animals by around 16 million years and indicated that trigonotarbids were among the earliest terrestrial animals.

Araneae

Great strides have been made recently in spider systematics (Coddington and Levi, 1991) and concomitantly, new finds of fossil spiders have added to the geological record. The oldest spider is *Attercopus fimbriunguis* Shear, Selden and Rolfe, 1987, from Gilboa; supposed spiders from Rhynie (Hirst, 1923) and Alken-an-der-Mosel (Stormer, 1976) have been disproved (Selden *et al.*, 1991). *Attercopus* is sister to all other spiders; the patella-tibia joint is a rocking joint but in a more plesiomorphic state than other spiders, lacking the 'compression zone Y' of Manton (1977). Autapomorphies of the *Attercopus* clade are: fimbriate paired claws, spinules on the palpal femur, and lack of trichobothria; the latter feature is puzzling.

In spite of descriptions of Devonian and Carboniferous araneomorph spiders (Archaeometidae Petrunkevitch, 1949; Pyritaraneidae Petrunkevitch, 1953), none of those seen by the author could be proved to be a spider at all. Petrunkevitch seemed to concur with Fritsch (1904) and Pocock (1911) in their placement of fossils in the Araneomorphae without question, even if he disagreed with their detailed descriptions. All of these authors seemed to place fossils in Araneomorphae on the basis of their general resemblance to particular groups of araneomorph spiders rather than real characters. For example, Petrunkevitch (1953:107) defined Pyritaraneidae and redefined Arachaeometidae as araneomorph spiders with segmented opisthosomae, differing from each other by their laterigrade and prograde legs respectively. Nowhere is the identification as araneomorphs questioned. Eskov and Zonshtein (1990a) considered segmentation of the opisthosoma in the Pyritaraneidae to be an artifact, but agreed that this family belongs in Araneomorphae. Selden *et al.* (1991) studied *Archaeometa nephilina* Pocock, 1911 in the British Museum (Natural History) and a plaster cast of *A. devonica* Stormer, 1976 from the Senckenberg Museum, concluding that neither species was a spider and that *A. devonica* may not be an arachnid at all. Carboniferous Arthrolycosidae Fritsch, 1904 and Arthromygalidae Petrunkevitch, 1923 in the British Museum (Natural History) can be placed with the mesotheles because of the distinct tergites on their opisthosomae. Eskov and Zonshtein (1990b) argued for a new group of Carboniferous 'labidognathous liphistiomorphs' on the evidence that the fossils lacked chelicerae yet any spider with orthognath chelicerae would have them preserved if the carapace and palps were. This argument presupposes that orthognath chelicerae are always porrect, which they may not be. To argue morphology from preservation (or lack of it!) is a dangerous practice.

Until recently, no mygalomorph spider was known earlier than the Tertiary. Eskov and Zonshtein (1990a) described some mygalomorphs from Siberia and Mongolia, placing them in the modern Mecicobothriidae, Atypidae and Antrodiaetidae. They are exceptionally well preserved, but poorly illustrated and described; in contrast, the line drawings are of high quality. In 1992, with the description of a Triassic mygalomorph, *Rosamygale*, our knowledge of the antiquity of mygalomorphs was more than doubled (Selden and Gall, 1992). This was placed in the extant family Hexathelidae, and suggests a widespread distribution of the family across Pangaea before rifting of the supercontinent. Hexathelids show many plesiomorphic characters among mygalomorphs but nevertheless, mygalomorphs may yet be found in Palaeozoic rocks.

Mesozoic spiders have only recently been discovered. The oldest fossil araneomorph is *Juraraneus rasnitsyni* Eskov, 1984, placed in a new family, Juraraneidae, in the Araneoidea. *Juraraneus*, like the mygalomorphs described by Eskov and Zonshtein (1990a), is well preserved but rather poorly documented for such an important find, so it is difficult to be sure whether the placement is justified. Eskov (1987) has also described Archaeidae from the Jurassic of Kazakhstan from where Filistatidae are currently being described (Eskov, 1990).

Recent finds of Cretaceous araneomorphs have emphasized the diversity of a spider fauna of modern aspect during this period. Unfortunately, some show little morphological detail (Jell and Duncan, 1986), but Selden (1990a) described specimens from the Lower Cretaceous of northeast Spain, beautifully preserved in lithographic limestone. The specimens included a deinopoid and a tetragnathid, so both cribellate and ecribellate orb-web weavers were in existence at this time. In broad terms, by the Tertiary, the spider fauna was almost identical to that of today, and only 3 families are known to have become extinct since the Palaeogene (Eskov, 1990).

Uropygi

Well preserved uropygids are found in Coal Measure rocks in Europe (e.g. Brauckmann and Koch, 1983) and North America. All are placed in the modern Thelyphonidae.

Schizomida

Three species of schizomids are known from the Pliocene 'Onyx Marble' quarries of Arizona and one from the Oligocene of China (Lin *et al.*, 1988).

Amblypygi

Fossil amblypygi are known from the Coal Measures of Europe and North America and from Tertiary ambers (e.g. Schawaller, 1979). Amblypygi may be present in the Devonian of Gilboa: a possible pedipalp tarsus was figured by Shear *et al.* (1984) and *Ecchosis pulchribothrium* Selden and Shear, 1991 may belong in this group (Selden *et al.*, 1991).

ARACHNID PHYLOGENY

Selden (1990b) discussed three recent phylogenetic hypotheses with the evidence of the fossil record (Fig. 3). A cladogram which accurately reflects evolutionary events predicts that successive dichotomies should occur in ascending chronological order, and a complete fossil record should show this. Weygoldt and Paulus's (1979) analysis (Fig. 3c) predicts that palpigrades should occur in strata at least as old as Devonian because the more derived mites and pseudoscorpions occur in beds of that age. In their scheme, Opiliones occupy a derived position. Van der Hammen (1989; fig. 3b) suggested that Opiliones should occur the Cambrian since they are tentatively shown as sister group to Xiphosura + Scorpiones. Shultz (1989, 1990; Fig. 3a) also placed Opiliones in a position which predicts their presence in Silurian times. Since scorpions were aquatic then, so would opilionids have been.

None of the phylogenetic analyses (Fig. 3) incorporated extinct groups. Whilst it is impossible to include ancestors in cladistic analyses, there is no reason why well known extinct groups should not be included, say at the Carboniferous level. Apart from the enigmatic palpigrades and the highly derived Schizomida, for which fossil evidence is lacking, all arachnid orders were in existence by that time.

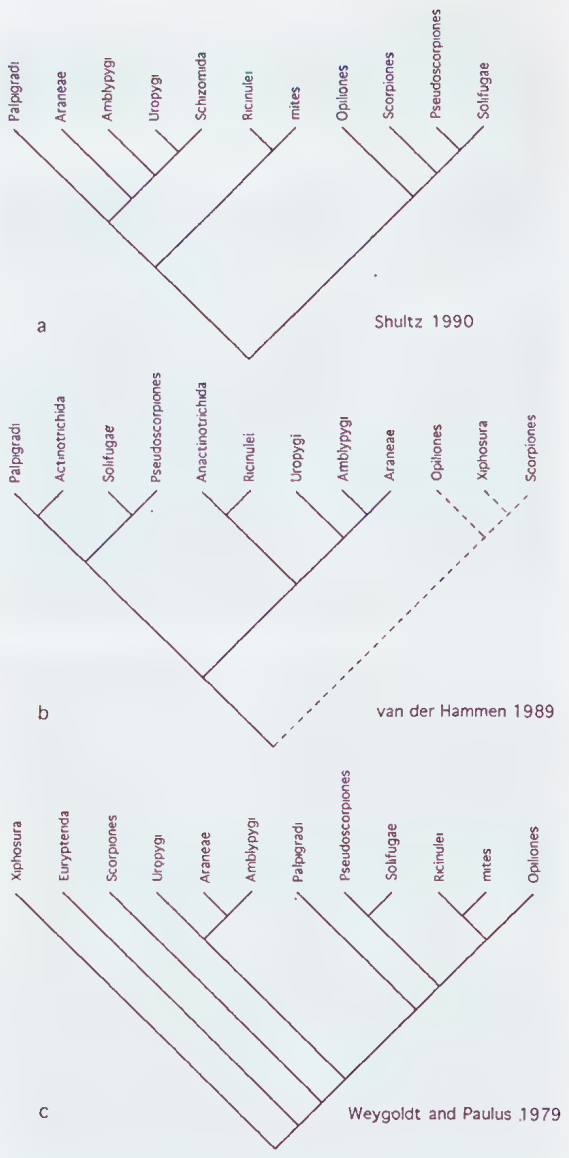

FIG. 3. Cladograms of relationships among the arachnid groups as viewed by a, Shultz (1990); b, van der Hammen (1989); and c, Weygoldt and Paulus (1979). Interrupted lines indicate uncertainty.

FUTURE PROSPECTS

Work in progress includes: palaeophysiology of early terrestrial chelicerates–aquatic and terrestrial adaptations in eurypterids, scorpions, and other Siluro-Devonian arachnids; palaeobiology of the Trigonotarbida; and Cretaceous spiders from Canadian amber and the Santana Formation of Brazil.

Much of Petrunkevitch's work needs revision. A new phalangiotarbid fauna has been collected in recent years from a coal mine tip in Somerset, England (Beall, 1991). Carboniferous Anthracomartida and Haptopoda need to be restudied, particularly in relation to the now extremely well known and possibly related trigonotarbids. The identity of described Amblypygi is in little doubt, but modern descriptions would be helpful. In need of critical examination are: the single fossil solifuge *Protosolpuga* from Mazon Creek, the supposed palpigrade *Sternarthron* from the Jurassic of Germany, and the amber spiders described by Petrunkevitch (e.g. 1942, 1950, 1958). The problem with these spiders is that over the years some of the supposed 'amber' in collections has discoloured, which suggests it may not be truly Palaeogene but rather more recent copal or other resins.

Successful palaeoarachnology requires knowledge of both Recent arachnids and understanding of styles of fossil preservation. Much previous work suffered from erroneous interpretations of one sort or another. Goals for future work are: to understand the origin of the present-day diversity of arachnids and the relationships among the various groups, and the reconstruction of ancient terrestrial ecosystems.

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SCORPIONS AS MODEL VEHICLES TO ADVANCE THEORIES OF POPULATION AND COMMUNITY ECOLOGY: THE ROLE OF SCORPIONS IN DESERT COMMUNITIES

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The diversity (5-16 species) and abundance (0.2-1.0 individuals/m^2) of scorpions suggest that they may be quite ecologically important in desert communities. Ecological importance is considered in terms of population energetics (the quantity of energy and mass flowing through populations) and of regulation of community structure and dynamics (influence on the distribution and abundance of other species). The energetic analysis provided three conclusions: 1) Scorpions monopolise a relatively large share of animal biomass, particularly relative to vertebrates and other arthropods. 2) This relative success is due to a suite of autecological traits (very low metabolism and very high assimilation efficiency leading to low energy requirements; and great tolerances to water stress, heat and starvation) that allows scorpions to prosper under the unpredictable and low food availability conditions that characterise deserts. 3) However, these traits lessen their impact on energetics, prey and competitors. Thus the importance of scorpions relative to homeothermic vertebrates is less than an analysis of density and biomass suggest because scorpions require and process prey in quantities relatively low to their biomass. Nevertheless, as a group, scorpions are probably important conduits of energy flow in deserts.

Research on the interactions among scorpions and between scorpions and spiders strongly suggests that scorpions can play key roles in the structure and dynamics of their communities. Studies in the deserts of California, Baja California and Namibia show that intraguild predation by scorpions is a major force determining the (temporal and spatial) distribution, abundance and age structure of populations of their competitors/prey.□*Araneae, Scorpionida, age structure, distribution, intraguild predation, population and community ecology.*

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Ecology is a rapidly developing area with a great deal of internal argument and disagreement. As in other fields, theory has advanced far more rapidly than empirical work. Consequently, much theory is controversial and in need of empirical evaluation. Scorpions possess a number of characteristics that make them ideal models to test and advance ecological theory. Thus, it is relatively easy to collect rapidly great amounts of data and to manipulate experimentally individuals and entire populations. Research on scorpions has contributed to many areas of population, behavioral and community ecology: e.g., the evolution of life history theory (Polis and Farley, 1980), the evolution and ecology of age-structured populations (Polis, 1984a, 1988; McCormick and Polis, 1986a), the dynamics of cannibalism (Polis, 1980a, 1981, 1984b), the dynamics of intraguild predation (Polis and McCormick, 1986b, 1987; Polis *et al.*, 1989), the evolution and ecology of foraging strategies (Polis, 1980b; Bradley, 1988), patterns and processes in biogeography (Due and Polis, 1986) and the patterns and processes affecting community and food web structure (Bradley, 1983; Polis, 1991a).

In this paper I evaluate the 'ecological importance' of scorpions. Throughout, I indicate how research on scorpions has advanced our general understanding of ecology. Although scorpions occur in almost all non-boreal habitats, I focus on desert scorpions because much evidence suggests that they may be particularly important components of arid ecosystems and are a relatively 'successful' group. They are diverse, some taxa are extraordinarily abundant, and, as a group, they form a large proportion of the biomass of all desert arthropods and easily exceed the biomass of all desert vertebrates. Their success arises partially because they exhibit several physiological and ecological traits that pre-adapt them to the low and unpredictable food levels of deserts.

'Ecological importance' can be expressed in terms of either energetics and nutrient cycling

(the quantity of matter and energy flowing through a population or functional group) or regulation of community structure and dynamics (the impact on diversity, distribution and abundance of other populations).

ENERGETICS AND NUTRIENT CYCLING

The importance of desert scorpions on energy and nutrient cycling is a function of the quantity of prey biomass captured. The amount of captured biomass is a function of the density, population biomass, metabolism and efficiency of energy transfer. I now present a very rough approximation of the relative importance of scorpions to the flow of energy and nutrients in desert ecosystems. To approach this question, data were compiled from the literature reporting the diversity, density and biomass of various groups of desert taxa (see Polis, 1990, 1991b; Polis and Yamashita, 1991 for additional details). These data are not without bias and other problems. For example, studies are not usually conducted in areas where the focal taxon is absent or rare; nor are rare species studied as often as common ones. Consequently, the statistics presented here overestimate density and biomass and should be taken as a first approximation of actual parameters. However, the data are instructive and suggest that scorpions could be a major link in the flow of energy through desert communities.

Group	Density (no./ha)	Diversity (no. species)	n
Mammals	43±130	28.5±21.3	14
Birds	0.6±1.1	46.7±27.3	14
Lizards	36.8±43	12±4.6	12
Insects	35,100±54,600	592±796	10
Termites	4,025,000±2,793,000	9.1±15	7
Isopods	241,810±336,850	1.3±0.8	7
Millipedes	1150±214	2.4±2.1	7
Spiders	3220±8800	54.4±26.7	31
Solpugids		9.9±6.7	37
Scorpions	3210±3500	7.1±2.5	58

TABLE 1. Estimated average density and diversity of major taxa of desert macrofauna reported from the literature. Diversity is the mean number of species per taxon from local sites in different deserts. Density statistics were standardized to a per hectare basis. Means are reported with their standard deviations; n = sample size. Note that these statistics should be viewed as very rough approximations rather than absolute values. Note that data on ants were insufficient to include here (see Polis and Yamashita, 1991 for further details).

How do desert scorpions measure against other groups of consumers for these parameters? First, scorpions are relatively speciose in deserts. On the average, 7.1 species co-occur in desert throughout the world (range: 2-16 sympatric species, typically, 5-9 species; Polis, 1990) (see Table 1 for comparison with other desert taxa). Furthermore, populations are often quite dense, averaging>3200 individuals/ha with several species maintaining populations 5000-10,000/ha (e.g., Shorthouse, 1971; Lamoral, 1978; Polis and Farley, 1980; Polis and McCormick, 1986a; Bradley, 1986; Polis, 1990). On the average, scorpions are reportedly more dense than all other macroscopic animal taxa in these deserts except 'insects', termites, and isopods (ants are undoubtedly also more dense) (Table 1). Since scorpions are among the largest of all terrestrial arthropods (adults of most desert species = 0.5-10g; Polis and Farley, 1980), these high densities produce rather large estimates of standing biomass (= density of individual species x mass of individual animal). Each species population of desert scorpion averaged 7.15 kg/ha. Only termites (and probably ants) support a greater population biomass per

Taxon	Population per species	Biomass (kg/ha) per taxon	n
Mammals	1.40	39.9	29
Birds	0.02	0.9	25
Lizards	0.57	6.8	46
'Insects'	0.88	521.2	31
Termites	12.45	113.4	7
Isopods	9.91	12.8	2
Millipedes	1.15	2.8	2
Spiders	0.13	7.1	4
Scorpions	7.15	50.8	17
All vertebrates		47.7	
All arthropods		708.1	
All macrofauna		755.8	

TABLE 2. Estimated population biomass for various taxa taken from literature. Population biomass per species is average wet weight of one species per hectare. This statistic was sometimes reported; however, it was often calculated by multiplying the average mass of an individual times the density. Population biomass per taxa is calculated as the product of population biomass per species and average diversity of that taxon. Note that data on ants were insufficient to include. Additional information is reported in Polis and Yamashita (1991). n refers to the number of species in a particular taxon for which biomass data exist. Note that these statistics are only gross approximations of reality.

species or per taxon (from the ordinal level down) than scorpions (Table 2).

When the biomass of all scorpions living sympatrically in desert areas is calculated (= mass of individual species x average number of sympatric species), scorpions as a group exhibit a greater biomass (= 50.8kg/ha) than all other taxa except termites (=113.4Kg/ha) and the sum of all other insects (= 521.2kg/ha; Table 2). Note also that the population biomass of scorpions is higher than any one group of vertebrates (e.g., mammals and lizards average 39.9 and 6.8Kg/ha) or all vertebrates combined (47.7kg/ha). Overall, scorpions form 6.7% of the biomass of all macrofauna species combined, 7.1% of the biomass of all macroarthropods and 106% of the biomass of all vertebrates.

Thus it would appear that they are important conduits for energy transfer in deserts. However, two characteristics lessen their importance. First, they exhibit the highest ecological (production) efficiencies (percent assimilated energy incorporated into new biomass) of all taxa that live in the desert (Table 3). Second, they exhibit metabolisms that are extremely low relative to other poikilotherms and endotherms (Table 4). Although these features are powerful adaptations that allow efficient use of food and partially explain the success of scorpions in deserts, they also function to decrease the amount of energy transferred. Thus a gram of scorpion does not process as much food as a gram of arthropodivorous vertebrate. Overall then, desert scorpions are less important in energy and nutrient cycling than their diversity, abundance and biomass suggest.

How much energy do desert scorpions process? We have two estimates. Polis (1988) calculated that average populations of *Paruroctonus mesaensis* used 9000 grams of prey/ha/year. The Australian *Urodacus yaschenkoi* requires 7900g/ha/year; this translates into 98,400 ants or 31,570 medium sized spiders eaten per hectare per year (Shorthouse, 1971; Marples and Shorthouse, 1982). It is uncertain exactly how such figures for individual scorpions or for the sum of all sympatric species of scorpions compare to those for vertebrates. This is an interesting question to pursue.

Group	P/A%
Insectivorous mammals	0.86
Birds	1.29
Small mammals	1.51
'Other' mammals	3.14
'Homeotherms'	3.1
Fish	9.77
Social insects	10.3
Terrestrial invertebrates*	25.0
Solitary herbivorous insects	38.8
Solitary detritivorous insects	47.0
Solitary carnivorous insects	55.6
Spiders	45-60
Scorpions	68.2

TABLE 3. Ecological (Production Efficiency) of various animal taxa. This efficiency is equal tothe proportion of assimilated energy that is incorporated into new biomass (=Production/Assimilation). Note that the highest efficiencies are found in carnivorous insects, spiders and scorpions. *Terrestrial invertebrates do not include insects or arachnids. (primarily from Humphreys, 1979; see Polis and Yamashita, 1991 for further details).

INFLUENCE ON COMMUNITY STRUCTURE AND DYNAMICS

The second measure of ecological importance is to determine how a taxon influences the dynamics, distribution and abundance of other taxa. In theory, scorpions can influence desert communities in many ways: as predators affecting characteristics of their prey, as prey of other predators and as competitors of other arthropodivores.

One of the basic questions in ecology is: 'What factors determine the distribution and abundance of species?' To approach this question, researchers often focus on groups of similar species that use similar resources; especially those resources the supply of which may be limiting and in demand (e.g., food). Such species groups

Taxon	Metabolic rate ($ml/O_2/gm/hr$)
Homeotherms (basal rates)	
Mammals	0.07-7.4
shrew	7.4
rodents	1.80
elephant	0.07
Birds	2.3-4.7
Poikilotherms (at 25°C)	
Insects	1.665 ± 1.25
Spiders	0.92 ± 0.92
Scorpions	0.057 ± 0.048

TABLE 4. Metabolic rates of various animal taxa. The data are taken from many sources. The sample size for insects is 82 species; for spiders, 8 species; and for scorpions, 7 species. (see Polis and Yamashita, 1991 for further details).

are called guilds (= a group of species that use resources in a similar way and are thus potential competitors). For example, guilds of desert granivores (birds, ants, rodents) all eat seeds, regardless of specific differences in resource acquisition.

One approach to study guilds is to describe their patterns or structure. By guild structure, we mean the diversity and abundance of species members; spatial and temporal patterns and resource use (i.e., niche characteristics). However, such descriptive studies, although common, are not fully satisfying because they do not directly address the processes that produce the observed patterns.

An alternative approach is to determine if guild members interact, and if so, can such interactions significantly shape guild structure. There are several possible ways that guild members can interact. These range from cooperation and mutualism to competition and even predation. Such predation among guild members is called intraguild predation (Polis and McCormick, 1987; Polis *et al.*, 1989). Intraguild predation is an ubiquitous interaction among many assemblages of potential competitor but has received little formal attention from either theorists or empiricists (Polis *et al.*, 1989).

One major theme of my research with scorpions has been to analyze the characteristics and significance of intraguild predation. Many scorpion prey items (other scorpions, spiders and solpugids) are also potential competitors with scorpions (Polis, 1990; Polis, 1991a, b; Polis and Yamashita, 1991). I present information on three systems; in each, scorpions frequently eat species in the same guild of arthropodivorous predators and such intraguild predation significantly affects the distribution, abundance and population dynamics of these potential competitors. I used scorpions in these studies as models to delineate the characteristics and dynamics of intraguild predation. These studies illustrate how scorpions have proved to be extraordinarily amendable for ecological research: large amounts of data can be collected, interactions (e.g., feedings) observed and quantified relatively easily, and individuals or whole populations manipulated experimentally. For example, in the first study, field data were collected on 130,000 individuals, 2000 feedings and 6000 individual scorpions were manipulated in controlled field experiments.

INTERACTIONS AMONG SCORPIONS IN THE COACHELLA VALLEY

Four species of desert scorpion co-occur in sandy habitats on the floor of the Coachella Valley (Riverside County, California). Three are in the family Vaejovidae (*Paruroctonus mesaensis* Stahnke, *P. luteolus* Gertsch and *Vaejovis confusus* Stahnke); one (*Hadrurus arizonensis* Ewing), the Iuridae (Polis and McCormick, 1986a, 1987). *Paruroctonus mesaensis* form >95% of all individuals and occur at densities in the range of 0.2-0.5 individuals/ha; the other three species are relatively rare. Each species requires 2-5 years to mature and is composed of several distinctly sized year classes. Size changes greatly, e.g., *P. mesaensis* increase 60-80 times in weight from 0.03g (instar 2) to 2.0-2.5g (non-gravid adults). The year classes and species overlap to various degrees in use of insect and arachnid prey; average overlap among all species is moderate to high (0.67 [prey size] and 0.43 [prey taxa]). Thus, the scorpions potentially compete for food.

Extensive intraguild predation occurs among the four species; Table 5 presents a matrix of who eats whom. Several factors characterize this intraguild predation: 1) Each species was both an intraguild predator and prey. Such mutual predation occurs simply because the predator scorpion was always larger regardless of the species combination involved (n= 170 scorpion-scorpion predations). Thus scorpions of all species are vulnerable as they grow from small juveniles to full size adults and predatory reversals (mutual predations) are common. For example, young *P. mesaensis* scorpions are eaten by relatively larger adult *P. luteolus* and *Vaejovis confusus*; adult *P. mesaensis* prey on the (now) relatively smaller adults of these species. Thus age/size is a key

	PREY				
PREDATOR	*H.ari*	*P.lut*	*P.mes*	*V.con*	Total
Hadrurus	0.0	6.3	12.5	3.1	21.9
P. luteolus	0.0	33.3	6.7	6.7	46.7
P. mesaensis	0.4	0.5	5.0	8.3	14.2
Vaejovis	0.0	0.0	8.0	4.0	12.0

TABLE 5. Scorpion-scorpion predation in the Coachella Valley. The entries represent the percent of the diet that each species forms as prey for each of the four scorpion species. The diagonal represents intraspecific predation (cannibalism) (from Polis & McCormick, 1987). *H.ari=Hadrurus arizonensis; P.lut = Paruroctonus luteolus; P.mes= Paruroctonus mesaensis; V.con =Vaejovis confusus.*

determinate of intraguild predation: adults are the predators and immature individuals are the prey significantly more frequently than expected by chance. 2) The most common species (*P. mesaensis*) was the predator in 91% of all intraguild predations observed. Its average overlap in prey use (= 0.44) with other scorpion species was second highest. 3) Intraguild predation, at least by *P. mesaensis*, is significantly more frequent when prey availability was low: when <1% of the population was feeding, heterospecifics formed 35% of all diet items. In contrast when the percent feeding was >5%, only 3.2% of all prey were other species of scorpion. 4) Mortality caused by intraguild predation was generally an inverse function of the density of both *P. luteolus* and *V. confusus*; this resulted because much of the surface activity of these two species occurred during (less productive) periods when *P. mesaensis* was absent from the surface. 5) Intraguild predation is important in scorpion population dynamics. When analyzed as percent mortality of small species (here = total number of individuals eaten by *P. mesaensis* divided by the total number ever observed), intraguild predation by *P. mesaensis* killed 8% and 6% of all *P. luteolus* and *V. confusus* ever observed.

Can such high rates of mortality cause the rarity of these species? It is only possible to approach this question using field experiments. Removal of >6000 *P. mesaensis* (=3.2Kg) from 300 (100m^2) quadrats over a 29 month period demonstrated that the rarity of these species is caused substantially by intraguild predation from *P. mesaensis*. 6) Both *P. luteolus* and *V. confusus* (but not *H. arizonensis*) increased significantly (600% and 135%) in removal as compared with 60 control quadrats. It was speculated that the rarity of the largest species (*H. arizonensis*) is a result of a bottleneck in adult recruitment; predation by *P. mesaensis* killed >10% of all newborn *H. arizonensis* observed during the study. 7) The age structure of these smaller species was significantly different in removal areas: first year juveniles were 1.75 to 2.85 more abundant in removals versus controls. This suggest that the numerical response by the rarer species would be even more dramatic if this experiment continued beyond its 29 month period. Note that a plausible alternative hypothesis exists: removal of *P. mesaensis* relaxed exploitation competition and thus allowed the observed increases in density. A robust test failed to detect competition in this system (Polis and McCormick, 1986b, 1987).

Thus, intraguild predation by *P. mesaensis* significantly depressed the abundance of the rarer species. Does intraguild predation likewise affect their distribution? Since predation is apparently a key factor in the population dynamics of these species, natural selection is expected to favor adaptations that reduce the probability that an individual will encounter its predator. Indeed prey often avoid places and times that their predators frequent or where the probability of predation is high (see Polis and McCormick, 1987). Typically, the large predatory entity (e.g., scorpion species and/or age class) occurs in productive periods and microhabitats whereas smaller entities coexist by spatial segregation in a heterogeneous habitat and by temporal displacement.

The temporal and spatial distribution of smaller age classes and species of Coachella Valley scorpions reflect avoidance (in ecological and/or evolutionary time) of larger age classes and species. The overall distribution of *P. luteolus* and *V. confusus* tend to place these species on the surface during times (in winter, late fall) and in places (off sand) characterized by relatively low surface populations of adult *P. mesaensis*. These times and microhabitats support significantly less prey than those used by adult *P. mesaensis*; consequently *P. mesaensis* has a feeding rate (2.95%) significantly greater than all other species combined (1.70%). Further, the minority of *P. luteolus* and *V. confusus* that forage when and where *P. mesaensis* is active suffer a disproportionately greater chance of being eaten by *P. mesaensis*. Intraspecific predation (cannibalism) has produced similar patterns of temporal distribution, feeding and mortality patterns among age classes of *P. mesaensis* (Polis, 1980, 1984a).

Thus, intraguild predation is an important factor limiting the abundance and shaping the distribution of these scorpions. Many other assemblages of desert scorpions exhibit patterns that suggest that scorpion-scorpion predation is a major process shaping distribution and abundance (Polis and McCormick, 1987; Polis, 1990; but see Bradley, 1988).

INTERACTIONS AMONG SCORPIONS, SPIDERS AND SOLPUGIDS IN THE COACHELLA VALLEY

Scorpions also frequently eat competitors other than other scorpions. For example, the diet of the scorpion *P. mesaensis* consisted of 8% spiders and 14% solpugids (Polis and McCormick, 1986b). Does such intraguild predation sig-

nificantly affect the distribution and abundance of these unrelated taxa? Spiders responded in the above experimental removal of >6000 *P. mesaensis* by doubling in removal quadrats as compared to controls. Surprisingly, neither solpugids nor all insects combined increased significantly (all $p > .05$) in removal plots. These taxa did not increase either because individuals dispersed from removal areas, because the increase of spiders and smaller scorpions compensated for the removal of *P. mesaensis* by eating surplus arthropods, or simply that scorpions exerted little impact on insect populations. The first explanation is likely true for widely foraging solpugids and is possible but unlikely for the more sessile insects. The second explanation is unlikely: the biomass increase of spiders and scorpions represented <10% of the removed *P. mesaensis* biomass. The third explanation, difficult to accept, is nonetheless a real possibility: *P. mesaensis* may take such a small proportion of all insects that its removal does not affect insect density.

INTERACTIONS BETWEEN SCORPIONS AND SPIDERS IN THE NAMIB DESERT

Predation by scorpions on spiders also appears to be a key determinant of spider densities in the Namib Desert (Polis and Seely, unpublished research, 1988, 1989). Both the scorpion *Uroplectes otjimbinguensis* (Karsch) (Buthidae) and the spider *Gandanimeno echinatus* (Purcell) (Eresidae) live under loose bark on larger *Acacia* trees and are the major arboreal predators of insects on such trees. Populations of *G. echinatus* are severely reduced when they co-occur locally on *Acacia erioloba* trees with the scorpion *U. otjimbinguensis*. This system is a model example how predator-prey interactions are complicated greatly by patterns of local distribution. Not all suitable patches (*Acacia* trees) contain the full array of local species capable of existing within the patch. Trees grow along the banks of dry rivers (e.g., the Kuiseb) and become less dense and more sporadic with increasing distance from the river bed. The local abundance of scorpions and spiders on each tree is a function of differential dispersal, extinction and a predator-prey relationship with *U. otjimbinguensis* scorpions eating *G. echinatus* spiders. Although both species are found on river trees, *U. otjimbinguensis* is, with no exceptions, the numerically dominant species (10-50 scorpions/trees) and *G. echinatus* is relatively uncommon (5-20/tree). This occurs because scorpions are effective predators on these spiders.

However, this outcome is more variable on isolated trees further from the river and along smaller washes entering the river. On some trees close to the river, the abundance of scorpions and spiders is similar to that found in the river. However, some trees have no scorpions and great numbers of spiders (50-400/tree); some trees have neither scorpions nor spiders; and some, no scorpions and few (<20) spiders. Overall, trees without scorpions support significantly more spiders (112.3 ± 60.6, $n = 21$) than trees with scorpions (24.5 ± 14.3, $n = 20$) ($p < 0.001$; only experimental trees scored). This variation in abundance and these distributions exist because neither *U. otjimbinguensis* nor *G. echinatus* disperse far from the river, yet spiders disperse further than scorpions. Dense spider populations occur only in more isolated trees where scorpions are absent. In trees quite distant from the river, neither species occur.

Does intraguild predation by *U. otjimbinguensis* scorpions on *G. echinatus* spiders produce such patterns of distribution and abundance? Additions of *Uroplectes* over a one year period to scorpion-free trees ($n = 11$) highly significantly ($p < .001$) reduced *G. echinatus* populations to 42% of that on control trees ($n = 12$). Removal of scorpions from trees ($n = 8$) also produced a highly significant, 2.9 times increase in *G. echinatus* as compared to control trees ($n = 12$) with their full complement of scorpions.

These experiments showed that intraguild predation was concentrated on young spiders and could significantly alter age distributions ($p < .001$ for each of the following comparisons): The smallest size class of spiders on experimental trees represented 49% of the population ($n = 728$ spiders) one year after scorpions were removed compared to only 31% ($n = 221$) on control trees where scorpions remained; similarly, the smallest size class formed 48% of all spiders ($n = 903$) on trees where scorpions were not present compared to 34% ($n = 820$) on those trees to which scorpions were added.

Thus differential dispersal and semi-deterministic biotic interactions combined with differing isolation of patches are major determinants of the distribution, abundance and age structure of these species. In general, historical and stochastic dispersal events in patchy environments are a paramount factor explaining the distribution and abundance of predators and their prey and species of competitors (Polis, 1991b; Polis and

Yamashita, 1991). Such conditions can produce local extinctions or great variance in abundances via deterministic biotic interactions, but promote global coexistence. I suspect that such situations are normal among many species living in the notoriously heterogeneous desert. Many such assemblages occur in patches; differential dispersal, local extinctions and 'hide-and-seek' dynamics are undoubtedly extremely important in determining the exact structure of local assemblages. Unfortunately, little research has focused on these processes. The system with scorpions and spiders on *Acacia* trees is ideally suited to analyze such processes and represent another example of the use of scorpions to advance our comprehension of ecological processes.

INTERACTIONS BETWEEN SCORPIONS AND SPIDERS ON ISLANDS IN THE GULF OF CALIFORNIA

This system shows several of the same general processes as the one on *Acacia* trees in the Namib and illustrates the importance of predator-prey interactions occurring between spatially structured populations. Spider, scorpion and/or lizard populations on small islands (approximately $<1km^2$) are 1-3 orders of magnitude more dense than on larger islands (approximately 1-$1000km^2$) and the mainland; significant negative relationships occur between island size and density for each of these taxa. For example, the scorpion *Centruroides exilicauda* is 2-25 times more abundant on small islands. Three major variables likely explain the great variance in spider abundance: 1) the presence of scorpion predators (often absent from small islands); 2) the dispersal and colonizing ability of spiders relative to scorpions (better colonizers of small islands as compared to scorpions); and 3) differential energy flow from marine to terrestrial systems (much greater to small islands).

This research has been in progress for four years (1989-1992) in the Midrift area of the Gulf on 41 island and 6 mainland sites between Bahia de Los Angeles (Baja California del Norte, Mexico) and Guaymas (Sonora, Mexico) (Polis unpublished). Scorpion and spider abundance were quantified at each site; spiders were counted on >4000 cacti (one sample unit) and $>8000m^2$ of supralittoral shoreline (another sample unit). Insect abundance was estimated at these sites for >1000 trap days.

Small islands ($<1km^2$) exhibit highly significantly greater secondary production of arthropods than larger islands and mainland areas. However, high productivity is not from autochthonous primary production by terrestrial plants. Evidence strongly suggests that allochthonous production from the ocean is the prime source of productivity. Many islands are 'desert islands' with limited primary productivity from terrestrial plants. Several of the most productive small islands support 2-28 plants (individuals, not species) yet 200-1000 spiders can occur on a single cactus!

Small islands are more productive than large islands and mainland areas for two reasons. First, the Perimeter : Area ratio of an island decreases with size (perimeter is a linear function; area, a square function). Thus small islands have relatively more shoreline per unit area of land and consequently, receive relatively more nutrient and energetic input from marine drift (shore wrack–algal and animal detritus). Second, species-area relations are such that small islands lack predators of nesting marine birds; thus small islands support large colonies of pelicans, gulls, petrels and terns.

Marine detritus and material from nesting birds are eaten by many (semi-) terrestrial arthropods. Some arthropods eat dead bird tissue (eggs, chicks, adults) and fish scraps. However, dipteran parasites are dense consumers of nesting birds and form an important conduit of energy from the sea to spiders. Trapping shows that insect abundance is highly significantly ($p<0.001$, all comparisons) greater in both supralittoral zones and around nests than other areas on these islands and on islands with colonies of marine birds compared to those without colonies (also see Due and Polis, 1985). Dietary analysis shows that detritivorous and parasitic arthropods act as conduits of energy from the sea when converted to large populations of terrestrial spiders, scorpions and/or lizards. For example, spiders are 2-5 times more dense on islands with colonies of marine birds versus those without colonies.

Predation is also an extremely important variable determining the abundance of these taxa. On Gulf Midrift islands, spider abundance is significantly lower in the presence of scorpions and lizards (particularly, *Centruroides exilicauda* and *Uta stansburiana*; 1990: $0.19/m^3$ cactus; 1991: $2.5/m^3$) versus their absence ($63.4/m^3$; $28.2/m^3$; both $p<.005$). The importance of scorpions but not lizards on spider abundance is suggested by the analysis of 10 islands near Guaymas in Sonora. Here, spider density is 38 times less

(0.41/m^3 cactus) on all islands with *C. exilicauda* (n=8) compared to those with lizards (15.3/m^3 cactus; n=2).

The final variables in this system are spatial structure and colonization ability. Incidence functions (percent occurrence on islands classified by area) describe the ability of taxa to disperse to and successfully remain on islands of different sizes. The incidence curves suggest that relative ability to colonize small islands roughly can be ranked: Spiders> *Uta* lizards> Scorpions> Nest predators >Songbirds. Colonization would be deterministic if a particular taxon were always present or absent for all islands of a particular size class. In fact, incidence values for smaller island size classes are neither 0 nor 100%, suggesting that presence or absence of a particular taxon is somewhat stochastic. Thus some small islands exhibit high densities of spiders because scorpions are absent whereas other similar sized islands exhibit low densities of spiders because scorpions are present.

An integration of colonizing abilities, productivity and predation is required to understand the distribution and abundance of these taxa. Each factor varies more or less regularly with island size: generally, as size increases, secondary productivity decreases, predation increases and the importance of differential colonizing ability diminishes. Multivariate analysis allows statistical dissection to determine the relative contribution of each of these factors to the observed variance in spider density. This analysis (Table 6) shows that spider density is a significant positive function of prey availability and significantly depressed in the presence of scorpions. Arthropodivorous lizards are a seemingly unimportant factor, explaining almost none of the variance in spider abundance on Midrift islands.

1990 data with lizards	df	SS	MS	F	p>F
Regression	4	3.25	0.81	8.67	0.0008
Error	15	1.42	0.09		
Total	19	4.65			
Perimeter: Area				10.3	0.0058
Scorpion presence				4.29	0.0559
Lizard presence				0.32	0.5827
Cactus volume				1.20	0.2902
Total R^2 this model =0.70					
1991 data with lizards	df	SS	MS	F	p>F
Regression	3	3.13	1.04	11.01	0.0004
Error	16	1.51	0.09		
Total	19	4.65			
Perimeter: Area				9.06	0.0083
Scorpion presence				5.80	0.0285
Lizard presence				3.76	0.9687
Total R^2 this model =0.674					

TABLE 6. Multivariate regression of factors that may influence spider abundance on islands in the Gulf of California in 1990 and 1991. The maximum R improvement technique is used; this produces the best model given all the independent variables. Independent variables include lizard presence, scorpion presence, perimeter: area ratio of island, mean cactus volume/island and prey availability/island. The best two variable model includes perimeter: area ratio and scorpion presence. Three variable models are presented with lizards. The effect of lizards is always non-significantly weak, regardless of what higher order model is used.

In summary: Productivity sets potential maximal population size. Small islands are much more productive than larger islands because of the relative greater input of marine allochthonous productivity from drift and marine birds. Colonizing ability establishes the insular species combinations; species-area relations show that larger islands are more diverse and support more types of predators. The realized abundance of terrestrial taxa is limited by (intraguild) predation. For example, if scorpion predators are absent, spiders are dense on small, high productivity islands. When scorpions are present, spider density is lower (but still higher than on large islands and the mainland) and the density of scorpions is relatively high. As island size increases, productivity decreases because nest predators are present (thus bird colonies disappear) and allochthonous detrital input decreases as a function of island Perimeter : Area ratio. Eventually, as island size increases (with decreases in productivity and increases in predation), the abundance of spiders, lizards and scorpions decreases until abundance on very large islands approaches that of the mainland. Strong predation from many sources occurs on the relatively low productivity mainland; consequently, populations of spiders, scorpions and lizards are quite low.

CONCLUSIONS

This paper presents various types of data to evaluate the 'ecological importance' of scorpions in deserts. Ecological importance was first considered in terms of population energetics (the quantity of energy and mass flowing through scorpion populations) and second, in terms of the regulation of community structure and dynamics (how intraguild predation by scorpions influen-

ces the distribution and abundance of their competitors/prey). The energetic analysis provided three conclusions: 1) Scorpions are quite diverse and abundant in deserts. They monopolize a relatively large share of animal biomass in desert communities, particularly relative to vertebrates and other arthropods. 2) Their relative success is due to a suite of autecological traits that are particularly suited to the harsh and variable climatic conditions of deserts. These traits (very low metabolism and very high assimilation efficiency leading to low energy requirements; and great tolerances to water stress, heat and starvation) preadapt them to prosper successfully under the unpredictable and low productivity food availability that characterize deserts. 3) However, these traits (low metabolism and high assimilation efficiencies) lessen their impact on energetics, prey and competitors. Thus the importance of scorpions relative to homeothermic vertebrates is less than an analysis of density and biomass suggest because scorpions require and process prey in quantities relatively low to their biomass. Nevertheless, as a group, scorpions are probably important conduits of energy flow in deserts.

The research on the interactions among scorpions and that between scorpions and spiders strongly suggests that scorpions can play key roles in the structure and dynamics of the communities in which they live. These studies showed that intraguild predation by scorpions was a major force determining the (temporal and spatial) distribution, abundance and age structure of populations of their competitors/prey. However, as an important caveat, these interactions must be viewed in the context of the environment in which they occur. Dispersal ability, spatial structure and productivity are just some of the possible important factors that moderate the predator-prey interaction between scorpions and their intraguild prey.

The role of all ecologists is to integrate these factors to produce a synthetic understanding of the processes and dynamics that structure natural communities. I suggest that scorpions are particularly suited for this task and will continue to be a productive vehicle to advance the theoretical and empirical body of ecology.

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INTER-SPECIFIC ASSOCIATIONS INVOLVING SPIDERS: KLEPTOPARASITISM, MIMICRY AND MUTUALISM

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Many spiders have life-styles that involve a relatively close and prolonged association with another species; for example, between a specialist predator and its prey species, or a species may rely on another for either protection from predators or providing a suitable place to live. In asymmetric relationships, where individuals of one species benefit at the expense of the other, each species may act as a selection pressure on the other species. This can result in the evolution of specific adaptations and counter-adaptations that are evident in at least three kinds of inter-specific associations between spiders. These associations, namely kleptoparasitism, mimicry and mutualism are reviewed here. Our understanding of the evolution of these fascinating systems remains limited, despite numerous anecdotal accounts, because only a few studies are experimental. The purpose of this review is two-fold: to illustrate the use of comparative and experimental studies for understanding the evolutionary significance of these inter-specific relationships, and to highlight those gaps in our knowledge that might benefit from this approach.□*Inter-specific associations, spiders, kleptoparasitism, mimicry, mutualism.*

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Individuals of one species can affect individuals of another as a result of competition, predation, parasitism or mutualism. The evolutionary implications of any association between two or more species depends critically on the frequency and nature of the interaction. For example, a species may be the prey of many species of generalist predators. While these predators may represent an important selective pressure favouring anti-predator responses in the prey species, the adaptations of the prey may have little impact on the reproductive success of the predators. In contrast, a predator that preys on only one species can be an important selective force favouring anti-predator adaptations in that species. In turn, the prey species anti-predator adaptations can exert a selective pressure on the predator, favouring improved predatory abilities. Thus, each species acts as a selection pressure on the other, favouring adaptations and counter-adaptations, perhaps leading to characteristics that are increasingly specific to the relationship. However, these improvements need not necessarily change the relative position of each protagonist (Dawkins and Krebs, 1979). The evolution of these specific adaptations and counter-adaptations depends on both the frequency of the interactions and the effects of each protagonist. Host- parasite systems provide a rich seam of examples of such evolutionary processes (e.g. Endler, 1986; Davies *et al.*, 1989; Toft *et al.*, 1991), but there is also some evidence for similar processes in predator-prey systems (e.g. Brodie and Brodie, 1991; Endler, 1991).

INTER-SPECIFIC ASSOCIATIONS IN SPIDERS

Research on the behaviour and ecology of spiders has, with a few notable exceptions, focussed on issues involving single species (e.g. Humphreys, 1988), including foraging behaviour (Reichert and Luczak, 1982; Vollrath, 1987a; Uetz, 1992), habitat choice (e.g. Reichert and Gillespie, 1986), intraspecific competition (e.g. Reichert, 1982), courtship and mating (e.g. Robinson and Robinson, 1982; Elgar, 1992) and social behaviour (Buskirk, 1981; Elgar and Godfray, 1987; Uetz, 1988). Nevertheless, some spiders have relatively specific and prolonged relationships with other species. These relationships often involve predation or avoiding predation, and perhaps a reason why inter-specific interactions involving spiders have been neglected is that spiders are frequently perceived as generalist predators; cursorial or wandering spiders attack any vulnerable prey that they can find, while web-building spiders simply capture any prey that is caught in their web. However, the view that spiders are generalist predators is mis-

leading. Many spiders prey on only a few species using foraging techniques that include building specialised webs; producing chemical compounds that attract prey; utilising the webs or capturing capabilities of other spiders; mimicking prey behaviour; and cooperative foraging (see reviews in Stowe, 1986; Nentwig, 1987). Clearly, the survival and reproductive success of both predator and prey will depend on their predatory and defensive behaviours, and the degree to which the predator depends on the prey as a source of food. Not all associations between spiders and other invertebrates are predator-prey relationships; some species depend on other species for protection from predators, or providing suitable places to live. This review will focus on three inter-specific relationships involving spiders: kleptoparasitism, mimicry and mutualism.

A detailed understanding of the nature of these inter-specific associations will benefit from both experimental and comparative studies. The former can provide insight into both the fitness effects of the association on individuals of each species, and the importance of particular species' traits for maintaining the association. Comparative studies can provide further insight into the selection pressures responsible for the evolution of the association; reveal the implications of these associations for other aspects of the species life-history characteristics; and help formulate ideas that can be subsequently examined experimentally (see Harvey and Pagel, 1992 for review). While emphasising the evolutionary dynamic nature of inter-specific associations, a central theme of this review is to illustrate the use of comparative and experimental studies for understanding these systems, and also to highlight those gaps in our knowledge of arachnid inter-specific associations that might benefit from this evolutionary approach.

KLEPTOPARASITIC ASSOCIATIONS

The webs of spiders are host to numerous insects, including flies, damselfies and wasps (see reviews in Vollrath, 1984, 1987b; Nentwig and Heimer, 1987). Most descriptions of these guests are anecdotal, and consequently the nature of the relationship is poorly understood. The webs of many spiders are also host to numerous other spiders that obtain food from prey caught in the host's web. These spider guests, commonly referred to as kleptoparasites, are represented in at least four families, including the Dictynidae, Mysmenidae, Symphytognathidae and Theridiidae (Table 1). Of these spiders, the genus *Argyrodes* (Theridiidae) is the best documented (see Vollrath, 1984, 1987b).

Evidence of Kleptoparasitism

Argyrodes were originally described as commensals: *Argyrodes* benefit by feeding on the prey items that are caught in the host's web, but the host is not disadvantaged because these prey items do not form part of its diet (e.g. Belt, 1874). However, subsequent behavioural and ecological studies revealed that individual *Argyrodes* remove prey that might otherwise be consumed by the predator. These observations suggest that the relationship between *Argyrodes* and their hosts is more accurately described as kleptoparasitic rather than commensal (see Vollrath, 1984, 1987b).

In fact, kleptoparasitism may also be an inappropriate description. A kleptoparasitic relationship implies that one partner in the symbiosis benefits at the expense of the other, and that the kleptoparasite has certain characteristics that are adaptations to this lifestyle. Studies of several species associations leave little doubt that the latter contention is correct. For example, the symphytognathid *Curimagua bayano* inhabits the webs of a large mygalomorph *Diplura*, either climbing about the funnel web or remaining on the host (Vollrath, 1978). After a *Diplura* has caught, masticated and enveloped a prey item in digestive fluids, the kleptoparasite descends to the prey item and imbibes the liquidized prey. Interestingly, the anatomy of the mouth of *C. bayano* apparently prevents it from being able to capture, hold or masticate its own prey, suggesting that it is an obligate kleptoparasite (Vollrath, 1978).

Several behaviours of *Argyrodes* appear to be adaptations that are specifically related to their kleptoparasitic lifestyle. These spiders can move throughout the web, apparently undetected by the host, and the attempts of the kleptoparasites to obtain prey items may vary according to the behaviour of the host (Vollrath, 1984, 1987b). There are several mechanisms by which kleptoparasitic *Argyrodes* avoid detection or capture by the host: many species drop from the web when challenged by the host, *A. antipodianus* swings away from the web when the host is agitated (Whitehouse, 1986), and *A. ululans* cuts holes in the tangle web of its social spider host *Anelosimus eximius*, forming a tunnel that apparently facilitates escape (Cangialosi, 1991).

Surprisingly, the evidence that the presence of *Argyrodes* has a negative effect on the reproductive success of the host has not been directly assessed. For example, there are no experimental evidence that the growth rate or fecundity of the host is reduced by the presence of *Argyrodes* (or any other genera of kleptoparasites). Instead, the negative impact of *Argyrodes* on its host has been inferred primarily from either the behaviour of the host (e.g. Larcher and Wise, 1985), or from estimates of the energetic costs derived from the loss of prey items obtained by *Argyrodes*. For example, the number of prey items consumed by *Nephila clavipes* is reduced with increasing numbers of *Argyrodes* on the web (Rypstra, 1981), and *A. ululans* removes around 26% of the prey items that are caught in the web of its host *Anelosimus eximius* (Cangialosi, 1990b). Vollrath (1981) examined the potential costs of *Argyrodes* by estimating the energetic requirements of a single kleptoparasite. The daily energy requirements of the 3-4 mg *A. elevatus* is 0.82 J, about 0.5% of the daily requirements of its 975mg (*Nephila clavipes*) host. This proportion increases with larger numbers of kleptoparasites per web; over 40 individuals have been counted on a single *Nephila* web (although the average is 2.2 kleptoparasites per web), suggesting a potentially high energetic cost of this relationship (Vollrath, 1981).

If kleptoparasites exact a cost on host reproductive success, then selection should favour any trait that enables the hosts to reduce that cost. There are several mechanisms by which hosts might reduce the cost of kleptoparasitism: recovering the prey from the kleptoparasite; reducing the kleptoparasites access to the prey; or simply abandoning the web and building another elsewhere. Interestingly, hosts appear to be inefficient at recovering prey (Vollrath, 1979a, b; Rypstra, 1981) although several host species reduce access to their prey by chasing the kleptoparasites (Cangialosi, 1990b) or concealing the prey in retreats (see Cangialosi, 1990b). Larcher and Wise (1985) demonstrated experimentally that hosts are more likely to abandon webs when *Argyrodes* are present than absent. *Nephila clavipes* relocates its web when it is infested with large numbers of kleptoparasites (Rypstra, 1981), although the behaviour of *N. clavipes* may be a response to lower feeding rates, rather than to numbers of kleptoparasites.

Social or communal spiders appear to have fewer defensive options against high kleptoparasite loads, and this cost may be higher if the number of kleptoparasites per web is greater in larger colonies. For example, *Nephila edulis* builds webs in aggregations, and webs in aggregations have higher kleptoparasite loads and infestation rates than those found alone (Elgar, 1989). Re-locating a web away from an aggregation may reduce kleptoparasite load, but the host subsequently does not benefit from the foraging and predator defense advantages of living within an aggregation (e.g. see Uetz, 1988). Moving web sites to reduce kleptoparasite load may not be possible for some social spiders, such as *Anelosimus* that build substantial, permanent webs. Indeed, high kleptoparasite loads are apparently responsible for the demise of some *Anelosimus* colonies (Cangialosi, 1990b) but not others (Vollrath, 1982).

Like their hosts, individual kleptoparasites may also react to variation in prey capture rates. The feeding rates of kleptoparasites are likely to be influenced by both the prey capture rate of the host and the number of other kleptoparasites on the web. Host web capture rates may vary according to both the location and the size of the web. The number of kleptoparasites increases with the web size of several host species (e.g. Elgar, 1989; Cangliosi, 1990a), possibly because larger webs have higher web capture rates that can support more kleptoparasites. Web-building spiders relocate their webs according to prey capture rates (e.g. Gillespie and Caraco, 1987), and *Argyrodes* may behave similarly by moving to different webs (but see Larcher and Wise, 1985). It would be interesting to establish experimentally whether the emigration rate of individual *Argyrodes* increases as a result of lower web capture rates or increased numbers of conspecifics. If the latter, it is possible that the distribution of *Argyrodes* within a population of hosts, particularly those hosts that aggregate, could be predicted by the ideal free distribution (see Milinski and Parker, 1991).

A possible option for kleptoparasites that experience a low feeding rate is to capture and consume the host before moving to the web of another host (e.g. Tanaka, 1984). Some species of *Argyrodes* are either obligate or facultative predators of their hosts (see Table 1). Predatory *Argyrodes* can capture the host through mimicking a prey item (e.g. Whitehouse, 1986) or simply advancing toward the host and attacking it. Such a specialised form of predation is not uncommon in spiders, and has been recorded in several families (e.g. Jackson, 1987; Jackson and Blest, 1982; Jackson and Brassington, 1987; Jarman

TABLE 1: Spiders that are presumed to be kleptoparasites of web-building spiders. Families: Ag, Agelenidae; Am, Amaurobiidae; Ap, Aphantochilidae; Ar, Araneidae; Cl, Clubionidae; Co, Corinnidae; De, Deinopidae; Di, Dipluridae; Er, Eresidae; Gn, Gnaphosidae; Lin, Linyphiidae; Lio, Liocranidae; Ph, Pholcidae; Pro, Prodidomidae; Sa, Salticidae; Td, Theridiidae; Tm, Thomisidae; Ul, Uloboridae; Zo, Zodariidae. Agg, Aggregates; Soc, Social; Sol, Solitary. Web types: O, orb; T, tangle; S, sheet; F, funnel; Sp, space.Body sizes in mm.

Kleptoparasitic taxa	Body size		Host					Guests per web	Assoc*	Source
	♂	♀	Family	Species	Size	Web	Social			
Dictynidae										
Archaeodictyna ulova			Er	*Stegodyphus*		T	Soc		K	Griswold & Meikle-Griswold (1987)
Heteropodidae										
Olios diana			Am	*Badumna candida*		T	Soc	20	K	Jackson (1987)
O. sp. indet.			Am	*Badumna candida*		T	Soc	10	K	Jackson (1987)
O. lamarcki			Er	*Stegodyphus sarasinorum*		T	Soc	10	K	Jackson (1987)
O. obesulus			Er	*Stegodyphus sarasinorum*		T	Soc	8	K	Jackson (1987)
Mysmenidae										
Isela okuncana			Di	*Allothele terretis*		F	Sol		K	Griswold (1985)
Kilifia inquilina			Di	*Thelechoris karschi*		F			K	Coyle *et al.* (1991)
Mysmenopsis archeri			Ph			T			K	Baptisa (1988)
M. capae			Ar	*Cyrtophora*		O			K	Baert (1990)
M. cidrelicola			Di						K	Coyle *et al.* (1991)
M. cienga			Ar	*Cyrtophora*		O			K	Baert (1990)
M. dipluroamigo			Di	*Diplura*		S			K	Vollrath (1978)
M. furtiva	1.5		Di	*Ischnothele xera*		T	Sol	14	K	Coyle *et al.* (1991)
M. gamboa			Di	*Diplura*		S			K	Vollrath (1978)
M. hauscar			Di						K	Coyle *et al.* (1991)
M. ischnamigo			Di	*Diplura*		S			K	Vollrath (1978)
M. monticola			Di	*Ischnothele* sp.		T	Sol	4	K	Coyle & Meigs (1989)
M. pachacutec			Di						K	Coyle *et al.* (1991)
M. palpalis			Di						K	Coyle *et al.* (1991)
M. tibialis			Di						K	Coyle *et al.* (1991)
M. sp. indet.			Di	*Ischnothele reggae*					K	Coyle *et al.* (1991)
Oonopidae										
Oonops pulcher	2.0	1.5	Am	*Amaurobius fenestralis*	8	T			K	Bristowe (1958)
Salticidae										
Simaetha paetula	7.0	7.0	Am	*Badumna candida*		T	Soc		KP	Jackson (1985)
Symphytognathidae										
Curimagua bayano	1.3	1.3	Di	*Diplura* sp.	40	S	Sol		K	Vollrath (1978)
Theridiidae										
Argyrodes antipodianus			Ag	*Cambridgea* sp.		F	Sol		KP	Whitehouse (1988a)
A. antipodianus			Ag	*Stiphidion*		F	Sol		KP	Whitehouse (1988a)
A. antipodianus			Am	*Badumna longinquus*		Sp	Sol		KP	Whitehouse (1988a)
A. antipodianus			Ar	*Araneus crassa*		O	Sol		KP	Whitehouse (1988a)
A. antipodianus			Ar	*Eriophora pustulosa*	13	O	Sol		KP	Whitehouse (1988a)
A. antipodianus			Ar	*Cyclosa trilobata*	8	O	Sol		KP	Whitehouse (1988a)
A. antipodianus			Ar	*Leucauge dromedaria*		O	Sol		KP	Whitehouse (1988a)
A. antipodianus			Ph	*Pholcus phalangioides*		Sp	Sol		KP	Whitehouse (1988a)
A. antipodianus			Td	*Achaearanea*		T	Sol		KP	Whitehouse (1988a)
A. antipodianus	3.0	2.5	Ar	*Cyrtophora hirta*	14	O	Sol		K	Elgar *et al.* (1983)
A. antipodianus	3.0	2.5	Ar	*Nephila edulis*	21	O	Agg		K	Elgar (1989)

Kleptoparasitic taxa	Body size		Host					Guests per web	Assoc*	Source
	♂	♀	Family	Species	Size	Web	Social			
A. argyrodes			Ar	*Cyrtophora citricola*		O			K	Vollrath (1984)
A. atopus	2.4	3.4	Ar	*Nephila clavipes*	25	O	Agg	5	K	Vollrath (1987)
A. attenuatus	17.0	9.3	none							Eberhard (1979a)
A. baboquinari	3.7	3.5	Td	*Latrodectus*		T	Sol		K	Exline & Levi (1962)
A. baboquivari	3.7	3.5	Ul	*Philoponella oweni*	6	O	Agg		KP	Smith Trail (1980)
A. cancellatus	3.2	3.8	Ag	*Agelenopsis*		F			K	Exline & Levi (1962)
A. cancellatus	3.2	3.8	Ar	*Argiope aurantia*	22	O			K	Exline & Levi (1962)
A. cancellatus	3.2	3.8	Ar	*Araneus strix*		O			K	Exline & Levi (1962)
A. cancellatus	3.2	3.8	Ar	*Mecynogea lemniscata*		O			K	Exline & Levi (1962)
A. cancellatus	3.2	3.8	Ar	*Metepeira labyrinthea*		O	Sol		K	Exline & Levi (1962)
A. cancellatus	3.2	3.8	Ar	*Nephila clavipes*	25	O	Agg		K	Exline & Levi (1962)
A. cancellatus	3.2	3.8	Ar	*Verrucosa arenta*	9	O			K	Exline & Levi (1962)
A. cancellatus	3.2	3.8	Li	*Frontinella pyramitela*	4	S			K	Exline & Levi (1962)
A. cancellatus	3.2	3.8	Ph	*Pholcus*		space	Sol		K	Exline & Levi (1962)
A. cancellatus	3.2	3.8	Td	*Theridion tepidariorum*	7	T			K	Exline & Levi (1962)
A. caudatus	3.1	3.9	Ar	*Argiope argentata*	16	O	Sol		K	Smith Trail (1980)
A. cochleaforma	2.7	3.7	Ar	*Argiope*		O			K	Exline & Levi (1962)
A. cochleaforma	2.7	3.7	Ar	*Gasteracantha*		O			K	Exline & Levi (1962)
A. colubrinus	25.0		none							Eberhard (1986)
A. cordillera	3.6	3.1	Ar	*Gasteracantha*		O			K	Exline & Levi (1962)
A. cylindratus			Ar	*Araneus ventricosus*		O	Sol		K	Shinkai (1988)
A. dracus	2.3	2.6	Ar	*Nephila clavipes*	25	O	Agg	5	K	Vollrath (1987)
A. elevatus	3.4	4.0	Ar	*Argiope argentata*	16	O		4	K	Vollrath (1979)
A. elevatus	3.4	4.0	Ar	*Gasteracantha*		O			K	Exline & Levi (1962)
A. elevatus	3.4	4.0	Ar	*Nephila clavipes*	25	O	Agg	5	K	Vollrath (1979
A. fictilium	10.0	5.0	Ar	*Araneus*		O			KP	Exline & Levi (1962)
A. fictilium	10.0	5.0	Li	*Frontinella communis*	4	S	Agg		KP	Wise (1982)
A. fictilium	10.0	5.0	Ul	*Philoponella oweni*	6	O	Agg		KP	Smith Trail (1980)
A. fictilium	10.0	5.0	none							Exline & Levi (1962)
A. fissifrons	7.0		Ag	*Agelena limbata*	16	F	Agg	2	KP	Tanaka (1984)
A. fissifrons	7.0		Lin	*Linyphia*		S			KP	Tanaka (1984)
A. fissifrons	7.0		Td	*Theridion japonicum*		T			KP	Tanaka (1984)
A. fissifrons	7.0		Ul	*Philoponella* sp.	3	O	Agg	3	KP	Elgar (pers obs)
A. fissifrons	7.0		Ul	*Uloborus varians*		O			KP	Tanaka (1984)
A. flagellum			none							Eberhard (1986)
A. globosus	2.3	2.3	Ar	*Nephila clavipes*	25	O	Agg		K	Exline & Levi (1962)
A. incisifrons			Ar	*Cyrtophora hirta*	14	O	Sol		K	Elgar *et al.* (1983)

Table 1. *continued*

Table 1. *continued*

Kleptoparasitic taxa	Body size		Host					Guests per web	Assoc*	Source
	♂	♀	Family	Species	Size	Web	Social			
A. incursus	3.8	2.2	Td	*Achaearanea mundula*	6	T	Sol	5	KP	Gray & Anderson (1989)
A. longissimus	24.0	19.0	none							Exline & Levi (1962)
A. miniaceus			Ar	*Nephila maculata*	43	O			K	Robinson & Robinson (1973)
A. nephilae	1.7	2.2	Ar	*Argiope*		O			K	Exline & Levi (1962)
A. nephilae	1.7	2.2	Ar	*Cyrtophora moluccensis*	19	O	Agg		K	Berry (1987)
A. nephilae	1.7	2.2	Ar	*Gasteracantha*		O			K	Exline & Levi (1962)
A. nephilae	1.7	2.2	Ar	*Neoscona*		O			K	Exline & Levi (1962)
A. nephilae	1.7	2.2	Ar	*Nephila*		O			K	Exline & Levi (1962)
A. nephilae	1.7	2.2	Ar	*Nephila maculata*	43	O			K	Robinson & Robinson (1973)
A. pluto	3.9	3.7	Ar	*Argiope aurantia*	22	O			K	Exline & Levi (1962)
A. pluto	3.9	3.7	Ar	*Metepeira labyrinthea*		O	Sol		K	Exline & Levi (1962)
A. pluto	3.9	3.7	Td	*Latrodectus*		T	Sol		K	Exline & Levi (1962)
A. proboscifo	2.6	2.9	Ar	*Gasteracantha*		O			K	Exline & Levi (1962)
A. projiciens	4.0	3.2	Ar	*Metazygia* sp.		O	Sol		KP	Eberhard (1986)
A. sp. A			Ar	*Nephila clavipes*	25	O	Agg	2	K	Rypstra (1981)
A. sp. B			Ar	*Cyrtophora moluccensis*	19	O	Agg		KP	Lubin (1974)
A. sp. C			Ar	*Gasteracantha*		O		23		Vollrath (1981)
A. subdolus	2.6	2.8	Ul	*Philoponella oweni*	6	O	Agg		K	Smith Trail (1980)
A. trigonum	4.2	2.5	Ag	*Agelena limbata*	16	F	Agg		KP	Suter *et al.* (1989)
A. trigonum	4.2	2.5	Ag	*Agelenopsis*		F				Exline & Levi (1962)
A. trigonum	4.2	2.5	Ar	*Mecynogea lemniscata*		O			KP	Wise (1982)
A. trigonum	4.2	2.5	Ar	*Metepeira labyrinthea*		O	Sol		KP	Larcher & Wise (1985)
A. trigonum	4.2	2.5	Lin	*Linyphia marginata*	5	S			KP	Exline & Levi (1962)
A. trigonum	4.2	2.5	Lin	*Neriene radiata*	5	S	Sol		KP	Larcher & Wise (1985)
A. trigonum	4.2	2.5	Td	*Latrodectus*		T	Sol			Exline & Levi (1962)
A. trigonum	4.2	2.5	Td	*Theridion zelotypum*	4	T			KP	Exline & Levi (1962)
A. trigonum	4.2	2.5	Lin	*Frontinella pyramitela*	4	S			KP	Suter *et al.* (1989)
A. ululans	4.0	3.7	Ar	*Nephila clavipes*	25	O	Agg		K	Exline & Levi (1962)
A. ululans	4.0	3.7	Td	*Anelosimus eximius*		T	Soc		K	Cangialosi (1990a)
A. weyrauchi	4.3	3.8	none							Exline & Levi (1962)

* Two categories of relationship ('Assoc') are defined: 'K' is Kleptoparasite only, and 'KP' means that the guest may also capture the host. Some species of *Argyrodes* may be incorrectly categorised as 'Kleptoparasite only' because their predatory behaviour has not yet been observed.

** Taxonomy of *Argyrodes* follows Levi and Exline (1962) and thus *Argyrodes*, *Ariamnes* and *Rhomphaea* are not distinguished.

	Body length†		t statistic
	kleptoparasite only	kleptoparasite and predator	
♀ *Argyrodes*	2.9±0.2 (14)	5.0±1.1(6)	3.41**
♂ *Argyrodes*	3.2±0.2 (14)	3.7±0.4 (5)	1.21
Dimorphism (♂/♀)	1.11±0.05 (14)	0.82±0.14 (5)	2.58*
Host	21.5±2.6	6.7±0.8 (5)	3.47 **

TABLE 2: Differences in kleptoparasite and host body length according to whether the kleptoparasite does or does not also prey on their host.
† values are mean lengths ± SE (sample sizes). Values compared using t-test with pooled variance. Average host body size measures were obtained for *Argyrodes* that have multiple hosts. * $p < 0.05$; ** $p < 0.005$.

and Jackson, 1986; Jackson and Hallas, 1990). A potential cost of this foraging strategy is that the kleptoparasite may become prey to the host. At least one host species has a relatively effective defensive behaviour: when the predatory *Argyrodes* is detected, the host simply cuts the web thereby collapsing it and ensuring that the predator cannot proceed further (e.g. Eberhard, 1979b). Suter *et al.* (1989) report that female *F. pyramitela* can discriminate between conspecific males, prey items and predatory *A. trigonum*, apparently using chemical cues, and respond accordingly.

Comparative Patterns Within *Argyrodes*

What evolutionary sequences are responsible for the diversity of predatory specialisations in *Argyrodes*? Smith Trail (1980) stresses the importance of the kleptoparasites' ability to identify the vibratory signals generated by the host, thus allowing them to stalk and safely capture the host. However, kleptoparasites that also attempt to capture their hosts risk being captured themselves. Consequently they may be more likely to attempt to capture vulnerable hosts, such as those that are smaller (e.g. Smith Trail, 1980; Larcher and Wise, 1985), moulting (e.g. Vollrath, 1984), or even the spiderlings of the host (e.g. Whitehouse, 1986).

If relative body size is important in determining the outcome of attacking the host, then predatory species of *Argyrodes* may be larger than primarily kleptoparasitic species, or the former may tend to specialise on smaller hosts. These predictions are supported by comparative data of body length measures for 20 species of *Argyrodes* (see Table 1). Species of *Argyrodes* were divided into two groups, according to whether they preyed on their hosts: females of *Argyrodes* that are only kleptoparasitic are significantly smaller than those that also prey on their hosts (Table 2). However, males of these two groups of species are not significantly different in body size (Table 2). *Argyrodes* that prey on their hosts also specialise on smaller hosts, compared with the size of the hosts of those species of *Argyrodes* that are only kleptoparasites (Table 2). These comparative data show that, as predicted, the difference in size between *Argyrodes* and its host is greater for those species that are primarily kleptoparasitic compared with those that are also predatory. These comparative data suggest that selection has either favoured larger body size for species that are both kleptoparasitic and prey on their hosts, or it has favoured a further reduction in body size in those species that are primarily kleptoparasitic. The latter argument is consistent with the view that kleptoparasitism is a specialised foraging strategy that evolved from a more general kleptoparasitic and predatory lifestyle (Vollrath, 1984).

The evolutionary sequence leading to the divergence of these two foraging strategies within *Argyrodes* is not known; one may have evolved from the other, or both may have diverged from a common web-building ancestor (see Whitehouse, 1986). Thus, it is not possible, without an accurate phylogeny, to establish whether selection has favoured an increase in body size with the predatory lifestyle, or a decrease in body size is associated with a kleptoparasitic lifestyle. Indeed, the species placed within the single genus *Argyrodes* by Exline and Levi (1962) have been placed by others into three genera; the *Ariamnes*, the *Rhomphaea*, and the *Argyrodes*. In this classification, the *Ariamnes* and *Rhomphaea* groups are primarily host-predators and the *Argyrodes* group are kleptoparasites (Whitehouse, 1987). Thus, the differences described above may be confounded by taxonomic associations (see below). Resolving some of these issues is most likely achieved by experimental manipulation of individuals within a species that shows both kleptoparasitic and predatory behaviour.

An additional pattern revealed by comparative analysis also deserves experimental investigation. The degree of sexual size dimorphism (male length/female length) covaries significantly with the foraging strategies of *Argyrodes*. Males are smaller than females in those species that prey on their host, consistent with patterns of size dimorphism in almost all other spiders (e.g. Elgar *et al.*, 1990; Elgar, 1991, 1992; Vollrath and Parker, 1992). However, males of those species of *Ar-*

Host taxa	Kleptoparasite*	Biology
Agelenidae		
Agelena (2), *Agelenopsis*, *Cambridgea*, *Stiphidion*	*Argyrodes* (4)	KP
Amaurobiidae		
Badumna (2)	*Simaetha*, *Argyrodes*	KK
Amaurobius	*Oonops*	K
Araneidae		
Araneus (5), *Argiope* (4), *Cyclosa*, *Cyrtophora* (2), *Gasteracantha*, *Leucauge*, *Mecynogea*, *Metazygia*, *Metepeira*, *Neoscona*, *Nephila* (3), *Verrucosa*	*Argyrodes* (18)	KP
Cyrtophora	*Mysmenopsis* (2)	KK
Dipluridae		
Allothele	*Isela*	K
Diplura, *Ischnothele*	*Mysmenopsis* (11)	KK
Diplura	*Curimagua*	K
Thelechoris	*Kilifia*	K
Linyphiidae		
Frontinella (2), *Linyphia*, *Neriene*	*Argyrodes* (4)	KP
Pholcidae		
Pholcus	*Argyrodes* (2)	KK
Pholcus'	Mysmenopsis	K
Theridiidae		
Achaearanea, *Theridion* (3), *Anelosimus*, *Latrodectus*	*Argyrodes* (7)	KP
Uloboridae		
Uloborus, *Philoponella*	*Argyrodes* (4)	KP

TABLE 3: Summary of taxonomic distribution of spiders that are host of kleptoparasites (see Table 1 for further details). KP= Kleptoparasites and predators; K=kleptoparasites. * No. species in each genus in parentheses.

gyrodes that are primarily kleptoparasitic are generally larger than their conspecific females (see Table 2). What factors are responsible for this reversal of size dimorphism patterns within this group of spiders? One explanation is that competition between males for access to females may be more intense for kleptoparasitic spiders, and consequently sexual selection has favoured large male size in these species (see also Whitehouse, 1988b).

There is considerable variation in both the number of species that are host to each species of kleptoparasite and the number of kleptoparasite species found on each web-building host species (see also Vollrath, 1984, 1987b). For example, *Argyrodes cancellatus* are found on the webs of at least ten different host species from five families (see Table 3), while the orb-weaver *Nephila clavipes* is host to at least seven species

	Host range		t statistic
	Kleptoparasite only	Kleptoparasite and predator	
No. species*	18	6	
Family	1.6±0.3	2.8±0.7	1.89
Species	2.7±0.7	3.5±1.3	0.57

TABLE 4: Mean host-ranges of *Argyrodes* that are either only primarily kleptoparasitic or they also prey on their host.* refers to *Argyrodes*.

of *Argyrodes*. It is likely that both host-range and parasite-range will expand as more records become available. In contrast, many species appear to be host specific, with one species of kleptoparasite recorded from the web of only one species of host. For example, in certain Peruvian habitats, *Argyrodes ululans* is found only on the webs of the social spider *Anelosimus eximius*, despite considerable effort searching for this kleptoparasite on other potential hosts (Cangialosi, 1990a).

Vollrath (1984) argued that *Argyrodes* can be placed in two general categories; specialists that are host specific but behaviourally versatile, and generalists that invade the webs of many different species but use relatively few techniques to obtain food. Thus, Whitehouse (1988a) considers *Argyrodes antipodianus* a specialist, primarily because its behaviour is versatile, and adults are found primarily on the webs of *Eriophora pustulosa*. Dichotomies like these can be misleading because both host-specificity and behavioural versatility are most likely continuous rather than discrete variables; *A. antipodianus* is found on the webs of several other hosts (Table 1). Furthermore, host-specificity may also vary between populations, depending on the diversity and abundance of potential hosts in different populations. For example, *A. antipodianus* in Whitehouse's (1988a) study may be found primarily on *Eriophora pustulosa* because that is the most common host in her New Zealand population.

The host range of *Argyrodes* may vary according to whether the species is both kleptoparasitic and predatory or whether it is only kleptoparasitic. Purely kleptoparasitic *Argyrodes* may escape host-detection through specialised behaviours, but these behaviours may be effective for relatively few host species. If so, the host ranges of primarily kleptoparasitic *Argyrodes* may be less than for species of *Argyrodes* that are also predatory. The comparative data provide little support for this prediction (Table 4); al-

though the host-range of primarily kleptoparasitic species is less than the range of predatory species, the difference is not statistically significant.

The results of these inter-specific comparative analyses within the genus *Argyrodes* should be interpreted cautiously. These patterns may be confounded by an association between foraging strategy and taxonomic affinity, and thus the differences in body size or host range may be due to other, unknown features that differ between these two groups. This possibility is especially relevant given the ambiguity of the taxonomic arrangement of this genus. Furthermore, some species of *Argyrodes* may be incorrectly assigned to primarily kleptoparasite status simply through lack of observations. Thus, the patterns may change when more data and/or a more accurate phylogeny become available. Nevertheless, the patterns suggest several interesting questions that could be resolved by an experimental approach.

Host Specificity Of Kleptoparasites

Both *Argyrodes* and *Mysmenopsis* belong to web-building families and thus are relatively close phylogenetically (Coddington and Levi, 1991). However, the range and taxonomic affinities of their hosts are substantially different (Table 1). *Argyrodes* have been recorded on the webs of 29 host genera from eight families (Agelenidae, Amaurobiidae, Araneidae, Linyphiidae, Pholcidae, Psechridae, Theridiidae, Uloboridae), and some species have many hosts (see above). In contrast, 11 of the 14 species of *Mysmenopsis* are found on diplurid hosts, with the remaining species found on *Cyrtophora* (Araneidae) and *Pholcus* (Pholcidae). A comparative analysis reveals a significant difference: every species of *Mysmenopsis* has only one host species, while the host range for *Argyrodes* is 2.7 ($\pm$0.7, n=18) species, or 1.6 ($\pm$0.3) host families.

Why is *Mysmenopsis* more host-specific than *Argyrodes*? There are several possible explanations. First, kleptoparasitism may have evolved more recently in *Mysmenopsis* than in *Argyrodes*, and therefore the former kleptoparasite has had less time to expand its host range. Second, the present associations between *Mysmenopsis* and diplurids may have evolved from a common ancestor and subsequently speciated as host/kleptoparasite pairs. Consistent with this is Coyle and Meigs (1989) description of two sister species of kleptoparasites (*Mysmenopsis monticola* and *M. furtiva*) that live on the webs of a pair of undescribed allopatric *Ischnothele* morphs that also appear to be sister species. Third, diplurids may be more sensitive to web invaders than the hosts of *Argyrodes*, and thus the kleptoparasitic behaviours required to avoid detection by one host species are not appropriate for another. In this regard, it is noteworthy that *Argyrodes* are not known to invade diplurid webs, despite the broad taxonomic range of their hosts.

The relatively permanent nature of the host's web is a common characteristic of the hosts of all kleptoparasites (Table 1). Kleptoparasites that live on permanent webs may benefit by spending less time searching for new webs compared with those that are associated with hosts that frequently move their webs. However, it may not be the permanent structure of the web that is important, but rather the tenacity of the web site. For example, the large, nocturnal, Australian orb-weaver *Eriophora transmarina* builds a new web every evening and then destroys it the following dawn. Despite the temporary nature of its web, this spider is also host to many individual *Argyrodes*, probably because it has a high web-site tenacity (M. Herberstein, unpublished data).

MIMICRY BY SPIDERS

Many species of animals, including spiders, resemble other, unrelated species. These resemblances may be visual, chemical, behavioural or acoustic and are usually referred to as mimicry. There are many different types of mimicry, which has precipitated some controversy over its definition (e.g. Endler, 1981; Pasteur, 1982). Two general forms of mimicry are distinguished in this review: defensive mimicry and aggressive mimicry. In the former, the mimetic form is presumed to have evolved because the risk of predation (or parasitism) on the mimic is reduced as a result of its resemblance to the model. The lower mortality occurs because the receiver (the predator) does not usually prey on the model, and fails to distinguish between it and the mimic. Aggressive mimics resemble some feature of their prey species, thereby increasing the chance of capturing the prey model. Both forms of mimicry occur in several families of spiders.

The relationship between mimic, model and receiver is asymmetric; only the mimic benefits and any improvement in the mimic will be favoured rapidly by natural selection. Both the model and the receiver may lose, in defensive mimicry, through increased attack rate and lost

	Spider taxon		Ant Taxa		Source
		Fam	Subfamily	Species	
ANT MIMICRY ONLY	*Castianeira dubium*	Cl	Ponerinae	*Pachycondyla obscuricornis*	Reiskind (1977)
	Mazax pax	Co	Ponerinae	*Ectatomma ruidum*	Reiskind (1970)
	Myrmecium bifasciatum	Co	Formicinae	*Camponotus femoratus*	Oliveira (1988)
	Myrmecium bifasciatum	Co	Myrmicinae	*Megalomyrmex modesta*	Oliveira (1988)
	Myrmecium sp.	Co	Ponerinae	*Pachycondyla unidentata*	Oliveira (1988)
	Myrmecium velutinum	Co	Ponerinae	*Ectatomma lugens*	Oliveira (1988)
	Myrmecotypus cubanus	Co	Formicinae	*Camponotus planatus*	Myers and Salt (1926)
	Myrmecotypus fuliginosus	Co	Formicinae	*Camponotus planatus*	Jackson & Drummond (1974)
	Myrmecotypus rettenmeyeri	Co	Formicinae	*Camponotus sericeiventris*	Reiskind (1977)
	Sphecotypus niger	Co	Ponerinae	*Pachycondyla villosa*	Oliveira (1988)
	Micaria pulicaria	Gn	Myrmicinae	*Acanthomyrmex niger*	Bristowe (1958)
	Micaria sp.	Gn	Myrmicinae	*Aphaenogaster beccarii*	Hingston (1927)
	Micaria scintillans	Gn	Formicinae	*Formica fusca*	Bristowe (1941)
	Phrurolithus festivus	Lio	Formicinae	*Lasius niger*	Bristowe (1941)
	Phrurolithus minimus	Lio	Formicinae	*Formica fusca*	Bristowe (1941)
	Martella furva	Sa	Formicinae	*Camponotus brevis*	Reiskind (1977)
	Martella furva	Sa	Formicinae	*Camponotus fastigatus*	Reiskind (1977)
	Myrmarachne elongata	Sa	Pseudomyrmecinae	*Tetraponera anthracina*	Edmunds (1978)
	Myrmarachne foenisex	Sa	Formicinae	*Oecophylla longinoda*	Edmunds (1978)
	Myrmarachne formicaria	Sa	Formicinae	*Formica rufa*	Bristowe (1941)
	Myrmarachne legon	Sa	Formicinae	*Camponotus acvapimensis*	Edmunds (1978)
	Myrmarachne lupata	Sa	Formicinae	*Polyrhachis*	Jackson (1986)
	Myrmarachne parallela	Sa	Ponerinae	*Pachycondyla carinulata*	Reiskind (1977)
	Myrmarachne parallela	Sa	Ponerinae	*Pachycondyla striatinodis*	Reiskind (1977)
	Myrmarachne plataleoides	Sa	Formicinae	*Oecophylla smaragdina*	Mathew (1954)
	Myrmarachne sp.	Sa	Formicinae	*Polyrhachis simplex*	Hingston (1927)
	Myrmarachne sp.	Sa	Formicinae	*Prenolepis longicornis*	Hingston (1927)
	Myrmarachne sp.	Sa	Myrmicinae	*Pheidole indica*	Hingston (1927)
	Sarinda linda	Sa	Formicinae	*Camponotus planatus*	Jackson & Drummond (1974)
	Synageles occidentalis	Sa	Formicinae	*Myrmica americana*	Cutler (1991)
	Synageles occidentalis	Sa	Formicinae	*Lasius alienus*	Cutler (1991)
	Synageles venator	Sa	Formicinae	*Lasius niger*	Engelhardt (1970)
	Synemosyna sp.	Sa	Pseudomyrmecinae	*Pseudomyrmex mexicanus*	Reiskind (1977)
	Synemosyna americana	Sa	Pseudomyrmecinae	*Pseudomyrmex boopis*	Reiskind (1977)
	Synemosyna aurantiaca	Sa	Pseudomyrmecinae	*Pseudomyrmex*	Oliveira (1988)
	Synemosyna smithi	Sa	Pseudomyrmecinae	*Pseudomyrma elongata*	Myers and Salt (1926)
	Synemosyna smithi	Sa	Pseudomyrmecinae	*Pseudomyrma flavida*	Myers and Salt (1926)
	Zuniga laeta	Sa	Formicinae	*Camponotus femoratus*	Oliveira (1988)
	Zuniga magna	Sa	Ponerinae	*Pachycondyla villosa*	Oliveira (1988)
	Anatea formicaria	Td	Myrmicinae	*Chelaner crocceiventre*	Reiskind and Levi (1967)
	Dipoena	Td	Myrmicinae	*Pheidole indica*	Hingston (1927)

TABLE 5 (part). Taxonomic distribution of spiders that mimic ants, including those that also prey on the model. * spiders observed with dead ants.Family abbreviations given in Table 1.

food respectively (see Endler, 1991), and natural selection will favour models that have less resemblance to the mimic (although the strength of this selection will depend on the frequency with which the model is attacked). The degree of resemblance between model and mimic that evolves will depend upon the benefits to the mimic and the costs of mimicry to the model. The costs to the model in aggressive mimicry are more complicated, and depend upon whether the model and the receiver (in this case, the potential prey) is the same individual.

	Spider taxon		Ant Taxa		Source
		Fam	Subfamily	Species	
ANT MIMIC AND PREDATOR	*Castianeira* sp.	Cl	Formicinae	*Camponotus paria*	Hingston (1927)
	Cosmophasis sp. 1	Sa	Formicinae	*Camponotus detritus*	Curtis (1988)
	Cosmophasis sp. 2	Sa	Formicinae	*Camponotus fulvopilosus*	Curtis (1988)
	Myrmarachne sp.	Sa	Formicinae	*Camponotus compressus*	Hingston (1927)
	Tutelina similis	Sa	Formicinae	*Camponotus*	Wing (1983)
	Not identified	Th	Formicinae	*Oecophylla smaragdina*	Cooper et al. (1990)
	Amyciaea albomaculata	Tm	Formicinae	*Oecophylla smaragdina*	Cooper *et al.* (1990)
	Amyciaea forticeps	Tm	Formicinae	*Oecophylla smaragdina*	Hingston (1927); Mathew (1954)
	Bucranium	Tm	Myrmicinae	*Cephalotes* (= *Cryptocerus*)	Bristowe (1941)
	Aphantochilus rogersi	Ap	Myrmicinae	*Zacryptocerus pusillus*	Oliveira and Sazima (1984)
	Habronestes bradleyi	Zo	Dolichoderinae	*Iridomyrmex purpureus*	R. Allan (pers. comm.)
	Zodarion	Zo	Myrmicinae	*Messor barbarus*	Hingston (1927)

Table 5. continued

Visual Mimicry: Spiders of Ants

Spiders that resemble ants are an especially intriguing form of mimicry that is poorly understood. Many of these spiders not only have an extraordinary physical resemblence with their ant models, but also exhibit particular behaviours that improves the illusion remarkably. Ant-mimics, represented in at least six families of spiders and mimicking the four major subfamilies of ants (Table 5), fall into two categories: those that appear to have little behavioural interaction with the ants and generally avoid contact with them; and those spiders that specialise on capturing and eating their ant models. There are no clear taxonomic affiliations between the species of spider mimics and the species of ant models; ponerine, myrmecine and formicine ants are models for both clubionid, salticid and other spiders. Nevertheless, certain species of ants appear to be models for spiders more frequently than others. For example, seven species of *Camponotus* are models to spider mimics and one species, *C. femoratus*, is a model for two corinnids (*Myrmecium*) and the salticid *Zuniga*; five species of the ponerine genus *Pachycondyla* are models for five different spiders, and the weaver ant *Oecophylla smaragdina* is a model for three species from Australia and India. It is not obvious why spiders mimic these genera of ants more frequently than others.

Some species of spiders mimic more than one species of ant. For example, the clubionid *Castianeira rica* resembles species of both ponerine and myrmicine ants and the different mimetic forms depend upon developmental changes, colour variation in adult females, and sexual dimorphism (Reiskind, 1970). Male *C. rica* resemble *Atta* and *Odontomachus*, while females resemble moderately large ponerines that are within the spiders' colour range. Furthermore, different instars of these spiders mimic ant models of equivalent size; thus the small, black early instars mimic small myrmicine ants, while the older instars resemble medium sized attine ants. Such a close degree of resemblance at different stages in the spiders' development suggests that the selection pressure favouring mimicry is very strong.

Ant mimicry can provide at least three benefits, depending upon whether the spiders prey on their ant models. These benefits include protection from various predators, improved predatory success on the ant prey, and both. Ant-mimics that apparently do not prey on their models are mostly salticids, corinnids and a few gnaphosids (Table 5). Mimics that prey on their models are mostly represented by thomisids and zodarids, although there are also a few records of theridiids, corinnids and salticids (Table 5). The record for the salticid species *Myrmarachne* (Hingston, 1927) is unusual and unlikely to be typical because other species of this large, ant-mimicking genus do not routinely prey on their model ants (e.g. Edmunds, 1978). Only a few genera of salticids are clearly regular ant-predators (e.g. Jackson and van Olphen, 1991, 1992). The theridiid *Dipoena* resembles the de-capitated head of a dead ant which are found in the refuse heap of the ant nest. Hingston (1927) suggests that mimicry in this species is aggressive because it allows the spider to live in the nest of the ants on whom it may prey. However, predation on these ant hosts by *Dipoena* was not observed.

Perhaps the most vexing question concerning defensive ant mimicry by spiders is establishing the identity of the receiver (i.e. the predator or

Spider		Ant		Source
Species	Family	Subfamily	Species	
Deinopis longipes	De	not specified		Robinson & Robinson (1971)
Chrysilla lauta	Sa	not specified		Jackson & van Olphen (1992)
Corythalia canosa	Sa	not specified		Jackson & van Olphen (1991)
Habrocestum pulex	Sa	Formicinae	*Lasius* sp., *Prenolepis* sp.	Cutler (1980)
Habrocestum pulex	Sa	Ponerinae	*Ponera pennsylvanica*	Cutler (1980)
Natta sp.	Sa	not specified		Jackson & van Olphen (1992)
Natta rufopicta	Sa	not specified		Jackson & van Olphen (1992)
Pystira orbiculata	Sa	not specified		Jackson & van Olphen (1991)
Siler semiglaucus	Sa	not specified		Jackson & van Olphen (1992)
Corythalia canosa	Sa	not specified		Edwards *et al.* (1975)
Euryopis californica	Td	Formicinae	*Camponotus*	Porter & Eastmond (1982)
Euryopis coki	Td	Myrmicinae	*Pogonomyrmex*	Porter & Eastmond (1982)
Euryopis funebris	Td	Formicinae	*Camponotus castaneus*	Carico (1978)
Latrodectus hesperus	Td	Myrmicinae	*Pogonomyrmex rugosus*	MacKay (1982)
Latrodectus pallidus	Td	Myrmicinae	*Monomorium semirufus*	MacKay (1982)
Steatoda fulva	Td	Myrmicinae	*Pogonomyrmex badius*	Hölldobler (1971)
Achaearanea sp.	Td	Formicinae	*Oecophylla smaragdina*	Cullen (1991)
Saccodomus formivorous	Tm	Dolichoderinae	*Iridomyrmex*	McKeown (1952)
Strophius nigricans	Tm	Formicinae	*Camponotus crassus*	Oliveira & Sazima (1985)
Zodarion frenatum	Zo	Formicinae	*Cataglyphis bicolor*	Harkness (1976)

TABLE 6: Spiders that specialise on ant prey but are not ant-mimics.Family abbreviations given with Table 1.

parasitoid). Despite widespread reports and descriptions of ant-mimicry by spiders, few studies have addressed this question quantitatively. The visual nature of ant-mimicry suggests that the spiders are gaining protection from visual enemies, including birds (e.g. Belt, 1874; Engelhardt, 1970), wasps (e.g. Edmunds, 1993) and other spiders (e.g. Cutler, 1991). It is unlikely that the visual resemblance to ants provides the spider mimics with protection from either their ant models or other species of ants, because ants perceive the environment primarily by chemical, rather than visual cues (see Hölldobler and Wilson, 1990). Furthermore, many spiders that are either specialist predators of ants (see Table 6) or live in close proximity with ants (Table 7) are not necessarily visual mimics.

Most of the diet of many spiders are other spiders (e.g. Bristowe, 1941, 1958; Reichert and Luczak, 1982; Nentwig, 1987). In contrast, ants are not a common prey item for most spiders, although a few spiders are specialist predators of ants (see Table 6). Thus, ant mimicry may provide some degree of protection from other spiders. Experimental evidence of this possibility is provided by Cutler (1991), who examined whether ant-mimicry in the salticid *Synageles occidentalis*, a mimic of the ant *Myrmica americana*, reduces the risk of predation by two other spiders *Tibellus* (Philodromidae) and *Phidippus* (Salticidae). These spiders do not feed on the ant *M. americana*, but more importantly they were less likely to attempt to capture the mimic *S. occidentalis* than immature *Phidippus* (that are not ant mimics).

Spiders are also prey to a variety of other invertebrates, especially pompilid and sphecid wasps (e.g. Coville, 1987), and acrocerid dipterans (e.g. Schlinger, 1987). These parasitoids are primarily visual hunters and many myrmecophilous arthropods gain protection against these enemies by associating with ants (e.g. Hölldobler and Wilson, 1990). Thus, ant-mimicry may reduce the risk of predation by sphecid and pompilid wasps. Edmunds (1993) provides qualitative data suggesting that ant-mimics *Myrmarachne* are less likely to be taken by the predatory wasp *Pison xanthopus* than might be expected if this wasp was indiscriminate in its choice of prey. Finally, it is interesting to note that no species of lycosid have been reported as ant-mimics (see Table 5), perhaps because these spiders are generally nocturnal foragers and are also seldom victim to sphecid wasps (see Coville, 1987).

Behavioural Mimicry: Courtship Vibrations

Some spiders are renowned for preying exclusively on other spiders. Notable among these

Spider		Ant		Source
Species	Family	Subfamily	Species	
Tetrilus arientinus	Ag	Formicinae	*Formica*	Bristowe (1958)
Eilica puna	Gn	Formicinae	*Camponotus inca*	Noonan (1982)
Acartauchenius scurrilis	Lin	Formicinae	*Tetramorium caespitum*	Bristowe (1958)
Cochlembolus formicarius	Lin	Formicinae	*Formica obscuripes*	Dondale & Redner (1972)
Evansia merens	Lin	Formicinae	*Formica fusca*	Bristowe (1958)
Masoncus	Lin	Formicinae	*Pogonomyrmex*	Porter (1985)
Thyreosthenius biovatus	Lin	Formicinae	*Formica rufa*	Bristowe (1958)
Phrurolithus	Lio	Formicinae	*Crematogaster*	Porter (1985)
Myandra	Pro	not specified		Main (1976)
Cotinusa	Sa	Dolichoderinae	*Tapinoma melanocephalum*	Shepard & Gibson (1972)

TABLE 7: Spiders that have been found within or adjacent to the nests of ants. Family abbreviations given with Table 1.

are the mimetid or pirate spiders that invade the webs and attack the owners of other species of spiders (e.g. Bristowe, 1941). Many of these spiders are aggressive mimics. For example, the mimetid pirate spiders *Mimetus* and *Ero* wait at the periphery of the web of the social spider *Anelosimus studiosus* (Brach, 1977). The mimetids then pluck on the web thereby attracting a host spider that is then captured and eaten. The salticid *Portia* is also well known for its ability to mimic the struggles of prey ensnared in the web of other spiders. The investigating host is then captured by *Portia* (Jackson and Hallas, 1990).

Some species of *Portia* also mimic the male courtship behaviour of their prey species; a behaviour that increases their chances of capturing the unsuspecting female (Jackson and Hallas, 1986). If prey populations suffer high frequencies of this form of mimicry, then *Portia* may act as a selection pressure favouring improved discriminatory abilities in the prey, thereby establishing an an evolutionarily dynamic 'arms race' (*sensu* Dawkins and Krebs, 1979). Evidence of this form of frequency dependent selection is provided by Jackson and Wilcox (1990, 1993), in their study of the predatory-prey relationship between two Australian salticids, *Portia fimbriata* and *Euryattus* sp.

Euryattus females live in a nest comprising a rolled-up leaf, suspended from rock ledges and tree trunks by silk guylines. *Portia fimbriata* is a versatile predator of many salticids and in a Queensland population, it preys on female *Euryattus* sp. using vibratory displays that apparently mimic the courtship behaviour of *Euryattus* males. This behaviour lures *Euryattus* females from their nest, and they are subsequently attacked by *P. fimbriata*. This specialised form of predation by *P. fimbriata* may be responsible for the improved ability of *Euryattus* to recognise and defend itself from *P. fimbriata*, compared with other salticids. For example, *Euryattus* recognises *P. fimbriata* as a potential predator, unlike another prey species *Jacksonoides queenslandica*. Interestingly, this recognition ability is not present in another population of *Euryattus* in which *P. fimbriata* are absent. Experimental trials reveal that *P. fimbriata* attacks and captures these 'naive' spiders more frequently than spiders from the population that is exposed to *P. fimbriata* (Jackson and Wilcox, 1993). It is still not clear whether the two populations of *Euryattus* are conspecifics or represent two different species. The more distantly related the two populations, the less likely that the differences in behaviour are the result of the presence or absence of *P. fimbriata*. Nevertheless, it appears to be a fascinating example of how the foraging behaviour of a predator has apparently acted as a selection pressure influencing the defensive behaviour of its prey.

Chemical Mimicry: Moths and Ants

Spiders produce a variety of chemicals that function to attract conspecifics. Female spiders from many different families produce pheromones that attract members of the opposite sex (e.g. Lopez, 1987; Pollard *et al.*, 1987), and Evans and Main (1993) show experimentally that pheromones may be important for maintaining social cohesion in social spiders. Several taxa of spiders are capable of inter-specific chemical communication, of which the most familiar is the remarkable form of chemical mimicry by bolas spiders (see Stowe, 1986, 1988 for extensive reviews). Bolas spiders, comprising several genera within the Araneidae, do not construct

orb-webs but instead swing at their prey a bolas (a droplet of adhesive) attached to the end of a silk thread. Bolas spiders are aggressive mimics and prey exclusively on male moths; the spiders produce a chemical substance that mimics the sex pheromone of its moth prey species (see Eberhard, 1977, 1980; Yeargan, 1988; Stowe, 1986, 1988; Stowe *et al.*, 1987). The exact source of the prey attractant compounds is not known, but is likely to be emitted from the spider (Stowe *et al.*, 1987). The evolution of this specialised foraging technique is particularly intriguing because it involves two phases; the first comprises the production of moth-attracting chemicals (see also Horton, 1979), and the second is the adoption of a specialised use of silk together with the loss of the orb-web. Interestingly, anecdotal observations suggest that the spider swings the bolas in response to vibratory signals generated by the flying moths (Main, 1976).

The mate location mechanism of at least seven families of moths are exploited by bolas spiders, but the range of moth prey species captured by each species of bolas spider varies (Stowe, 1986, 1988; Stowe *et al.*, 1987). Some spiders capture only one species of moth, while *Mastophora cornigera* is capable of capturing at least nineteen moth species (Stowe *et al.*, 1987). There are no obvious taxonomic affinities between the different groups of bolas spider and their moth prey species (Stowe, 1986, 1988). The variation in bolas spider prey-specificity is likely to be related to the bio-geographic distribution of potential moth prey, the chemical compounds produced by the spiders and the chemicals used as moth sex-attractants. Furthermore, some compounds that attract certain species of moth may inhibit attraction of other moths (Stowe *et al.*, 1987).

Since araneid spiders are capable of chemical mimicry of moths, it is not unreasonable to expect that ant-mimicking spiders may be capable of producing chemical compounds that 'appease' ants. Many species of invertebrate myrmecophiles produce chemicals that mimic ant communication chemicals (see Hölldobler and Wilson, 1990). The production of these chemicals can reduce the risk of the ants attacking the myrmecophiles. One group of spiders that are likely to be capable of chemical mimicry are those that live in ant nests (see Table 7). Little is known about these spiders, but some earlier reports may have mistakenly recorded them living in ant nests, rather than adjacent to the nest (see Bristowe, 1941). It is not clear whether these spiders prey on the ant larvae within the ant nest, or simply take advantage of a safe refuge. Whatever the reason, it is unlikely that they could remain in or near ant nests without some chemical protection, because ants rarely tolerate foreign nest intruders. Porter (1985) provided qualitative evidence for the presence of ant recognition pheromones by introducing myrmecophilous spiders *Masoncus* into the nests of different *Pogonomyrmex* ants. *Masoncus* were not attacked if they were re-introduced into their original nests, but the spiders were attacked and killed within minutes if they were placed in the nest of foreign *Pogonomyrmex* or other species of ants. It is not known whether these spiders actively produce the appropriate pheromones, or whether they simply adopt it from the substrate of the nest.

The predatory behaviour of two Australian spiders may also involve chemical mimicry. The Australian basket-web spider *Saccodomus formivorous* (Thomisidae) builds a basket-like web that appears to attract wandering *Iridomyrmex* ants that may venture into the basket web (McKeown, 1952). The spider also taps the ant with its legs, that may further mimic ant communication, and eventually captures the unsuspecting ant. It remains to be seen if *S. formivorous* webs capture only *Iridomyrmex* ants, and whether the ants are actively attracted to the basket-web. The extraordinary predatory relationship between an undescribed theridiid and its weaver ant *Oecophylla smaragdina* prey (see Cooper *et al.*, 1990) may also represent an example of the use of chemical mimicry. This theridiid constructs a web made of several strands of silk suspended between vegetation and additional strands that are anchored to the substrate below. The anchor part is a small white bead of silk that is very attractive to the ants. If the web is complete and an ant bites the silk it is catapulted into the web above, where it is captured by the spider. The bead of silk is often placed near ant 'highways' and can sometimes attract the attention of many individual *O. smaragdina* that all attempt to bite the silk.

MUTUALISTIC ASSOCIATIONS

There are few examples of mutualistic associations between species of spiders or even between spiders and other organisms. This is surprising, given the widespread occurrence of mutualistic associations in other taxa (e.g. Boucher *et al.*, 1982; Smith and Douglas, 1987; Hölldobler and Wilson, 1990), but may reflect the predatory nature of spiders. Tietjen *et al.* (1987) describe an

interesting example of a mutualistic association involving the social spiders *Mallos gregalis*. These spiders do not remove the remains of prey from their nest, and this debris becomes a nutrient base for various yeasts. The odour of these yeasts is apparently attractive to various flies, that settle on the prey carcasses and are then captured by the spiders. The association is likely to be mutualistic because the spiders provide food for the yeast and the yeast's presence attracts food for the spider.

The relationship between spiders that live in ants' nests and their ant hosts may also be mutualistic for some species. For example, Shepard and Gibson (1972) found myrmecophilous salticid spiders of the genus *Cotinusa* in 61% of 50 nests of the dolichoderine ant *Tapinoma melanocephalum*. Interestingly, ant nests with *Cotinusa* had more brood per nest, more workers per nest and more brood per worker than those nests without *Cotinusa*. Unfortunately, these differences were not examined statistically, and the greater numbers of ants and brood in the nests with *Cotinusa* may be due to the larger size of the former nests. Nevertheless, Shepard and Gibson (1972) suggest that the spider uses the ant nest as a foundation for the construction of its web, and in return provides the ants with some protection from predators or parasites.

Psechrus and *Philoponella*

Many species of orb-weaving spiders in the genus *Philoponella* (Uloboridae) build their webs within the barrier webs of other araneid, theridiid, agelenid and psechrid spiders (Struhsaker, 1969; Lubin, 1986). These associations were thought to be commensal; *Philoponella* has a place to build a web, but it was assumed that their presence has little effect on the host spider (e.g. Lubin, 1986).

In Madang Province, Papua New Guinea a species of *Philoponella* builds webs between the threads of the tangle web of a large psechrid *Psechrus argentatus*. Not all *Psechrus* webs have *Philoponella*, but as many as 15 males and females can be found on a single host web. Like many small uloborids, *Philoponella* is a communal spider, with several orb-webs sharing support threads. A theridiid *Argyrodes fissifrons* also patrols the barrier web but is never found on the sheet web of the host spider. The number of both *A. fissifrons* and *Philoponella* on a single host web is positively correlated with the size of the host.

The relationship between *P. argentatus* and *Philoponella* appears to be mutualistic (Elgar, unpublished). The growth rate of *P. argentatus* was significantly reduced following experimental removal of both *A. fissifrons* and *Philoponella* from the barrier-web. The lower growth rate during the ten day experimental period may represent a potential reproductive loss of around 30 eggs (estimated from the weights of egg masses). *P. argentatus* probably benefits by increased capture rates as a result of the increased area of tangle web generated by the webs of *Philoponella*, in a way analogous to the webs of some social spiders (see Struhsaker, 1969; Uetz, 1988). The additional webs may increase the probability of arresting insects that then drop into the sheet web, without being caught in the orb-web of *Philoponella*. It seems unlikely that *P. argentatus* benefits from the presence of *A. fissifrons*. In fact, *A. fissifrons* is more likely to have a negative effect on the host because it feeds on prey items caught in the barrier web and also may prey on *Philoponella*: on two occasions, *A. fissifrons* were seen feeding on *Philoponella*, consistent with other reports of the foraging behaviour of this species (see Table 1).

SOME CONCLUSIONS AND PROSPECTS

The relationship between kleptoparasitic *Argyrodes* and their hosts has been extensively examined, yet the effects of the association on the fitness components of either *Argyrodes* or its host are presently unquantified. Consequently, it may be inappropriate to call these species kleptoparasites because (a) they may not take prey that the host would otherwise feed on and (b) their hosts may not suffer a fitness cost. Of course, many other well documented host-parasite systems similarly fail to quantify the fitness effects of the presumed parasite (see Toft *et al.*, 1991). Nevertheless, circumstantial evidence that the presence of *Argyrodes* has influenced the biology of at least a few host species suggests that kleptoparasitism is an evolutionarily dynamic relationship. Comparative analyses reveal interesting differences in the biology of kleptoparasites that do, or do not, also prey on their host. However, there are no obvious explanations for the evolution of this behaviour.

There are interesting parallels between chemical mimicry by the bolas spider and vibratory mimicry by the salticid *Portia*; both are examples of aggressive mimicry in which the mimic exploits the mate-attracting mechanism of the model. They also illustrate the broad spectrum of sensory mechanisms that are exploited and the range of phylogenetic similarity between model

and mimic. The models are clearly disadvantaged by the mimics, and selection is likely to favour mechanisms that allow the victims to distinguish between their conspecific mates and the spider predators. There is some evidence of this selection for *Euryattus*, the model of *Portia*, but there are no data on the impact of bolas spiders on their model moth populations (but see Yeargan, 1988), nor is it known whether the ability of male moths to discriminate between conspecific female pheromones and bolas spider mimics has changed. One difference between these two mimicry systems is that the victims of *Portia* are female, but the victims of bolas spiders are male. This difference may have implications for the relative strength of selection in these types of aggressive mimicry, and the degree to which the model and mimic have undergone an evolutionary arms race.

Defensive mimicry of ants by spiders is taxonomically widespread but has received little experimental attention, compared with studies of other invertebrate taxa (e.g. McIver, 1987). In almost all cases the receiver is not identified and the fitness cost to the ants, as a result of defensive mimicry by these spiders, has not been quantified. Nevertheless, the degree of visual mimicry in many spiders suggests that there has been strong selection for this form of protection against predators. The inter-specific variation in the degree of resemblance between spider mimics and their ant models suggests an evolutionary process reflecting differences in the discriminatory abilities of the receivers. These differences may also reflect the frequency with which the spiders and ants co-occur, and the kind of substrate on which both are found. Finally, ant mimicry by spiders that also prey on their models begs the question of whether specialisation on ant prey followed ant mimicry, or vice-versa.

Mutualisms involving spiders have received little attention, compared with other inter-specific associations. There are several explanations: the Araneae may be characterised by an absence of mutualisms; these mutualisms simply have not been detected; or non-mutualistic associations may even have been incorrectly inferred. For example, the impetus of my study of *Psechrus*, *Philoponella* and *Argyrodes* was to reveal the fitness costs to the host of what appeared to be a kleptoparasitic relationship. The correct nature of the relationship between the species was only revealed experimentally, and this is likely to be true of many other inter-specific associations described in this review. But irrespective of the true nature of these relationships, inter-specific associations involving spiders provide a rich seam of biological systems that pose a variety of fascinating questions.

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VERTICAL DISTRIBUTION AND ABUNDANCE OF PSEUDOSCORPIONS (ARACHNIDA) IN THE SOIL OF TWO DIFFERENT NEOTROPICAL PRIMARY FORESTS DURING THE DRY AND RAINY SEASONS

JOACHIM ADIS AND VOLKER MAHNERT

Adis, J. and Mahnert, V. 1993 11 11: Vertical distribution and abundance of pseudoscorpions (Arachnida) in the soil of two different neotropical primary forests during the dry and rainy seasons. *Memoirs of the Queensland Museum* **33**(2): 431-440. Brisbane. ISSN 0079-8835.

Pseudoscorpions were extracted from 0-14cm soil depth in two dryland (upland) forests near Manaus, Brazil. In a primary forest on yellow latosol, about 1700 specimens per m^2 were obtained during the dry season and 1135 during the rainy season. They accounted for 10-15% of all arthropods extracted, excluding Acari and Collembola. In a primary forest on white sand soil (campinarana), about 530 specimens per m^2 were obtained during the dry season and 480 during the rainy season. They accounted for only 3-4% of all arthropods extracted, again excluding Acari and Collembola. Significant but different correlations were found in both forest types between the abundance of pseudoscorpions and changing moisture, temperature and pH conditions in relation to soil depth and season. Neither during the dry season nor during the rainy season was the abundance of pseudoscorpions in mineral subsoils higher in response to the changing soil moisture content in organic layers. This was reported for arthropods from forests in the seasonal tropics where periods without precipitation occur. Results are discussed at the species level. They are compared with published data on the vertical distribution and abundance of pseudoscorpion species from the yellow latosol of a secondary dryland forest (dry season and rainy season) from the same region.

In zwei Festlandwäldern in der Umgebung von Manaus wurden Pseudoskorpione aus 0-14cm Bodentiefe extrahiert. In einem Primärwald auf gelbem Latosolboden wurden während der Trockenzeit 1700 und während der Regenzeit 1135 Individuen pro m^2 nachgewiesen. Sie repräsentierten 10-15% aller extrahierten Arthropoden, Acari und Collembola ausgenommen. In einem Primärwald auf Weißsandboden (campinarana) wurden während der Trockenzeit 530 und während der Regenzeit 480 Individuen pro m^2 nachgewiesen. Sie repräsentierten nur 3-4% aller extrahierten Arthropoden, Acari und Collembolen wiederum ausgenommen. Signifikante aber unterschiedliche Korrelationen ergaben sich in beiden Waldtypen zwischen der Abundanz der Pseudoskorpione und der sich ändernden Feuchte, der Temperatur und dem pH in Bezug auf Bodentiefe und Jahreszeit. Weder während der Trockenzeit, noch während der Regenzeit, war die Abundanz der Pseudoskorpione im mineralischen Unterboden als Folge auf die sich ändernde Feuchte im organischen Oberboden höher. Dies wurde für Arthropoden in Wäldern der saisonalen Tropen, die Trockenperioden durchlaufen, nachgewiesen. Die Ergebnisse werden auf Artniveau diskutiert. Sie werden mit publizierten Daten über die Vertikalverteilung und Abundanz von Pseudoskorpionarten aus einem Sekundärwald auf gelbem Latosolboden im gleichen Gebiet verglichen.

□*Pseudoscorpiones, abundance, seasonality, vertical distribution, Neotropics.*

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In those wet but markedly seasonal tropics where periods without precipitation occur, terrestrial arthropods are reported to migrate to mineral subsoils in the dry season as a response to changing humidity in organic layers (Beck, 1964; Bullock, 1967; Goffinet, 1976; Lawrence, 1953; Levings and Windsor, 1984; Liebermann and Dock, 1982; Merino and Serafino, 1978; Petersen and Luxton, 1982; Rybalov, 1990; Strickland, 1947; Willis, 1976 and others). Central Amazonian dryland (= non-flooded upland) forests experience a rainy season (December-May; average monthly rainfall 211-300mm) and a 'dry' (= drier) season (June November; average monthly rainfall 42-162mm). Annual precipitation is 2105mm (based on 75 years of records from the meteorological station at Manaus, cf. Ribeiro and Adis, 1984). About 75% of the rainfall (1500mm) is recorded during the rainy season. This had no observable difference in vertical distribution of terrestrial arthropods in primary forests on yellow latosol

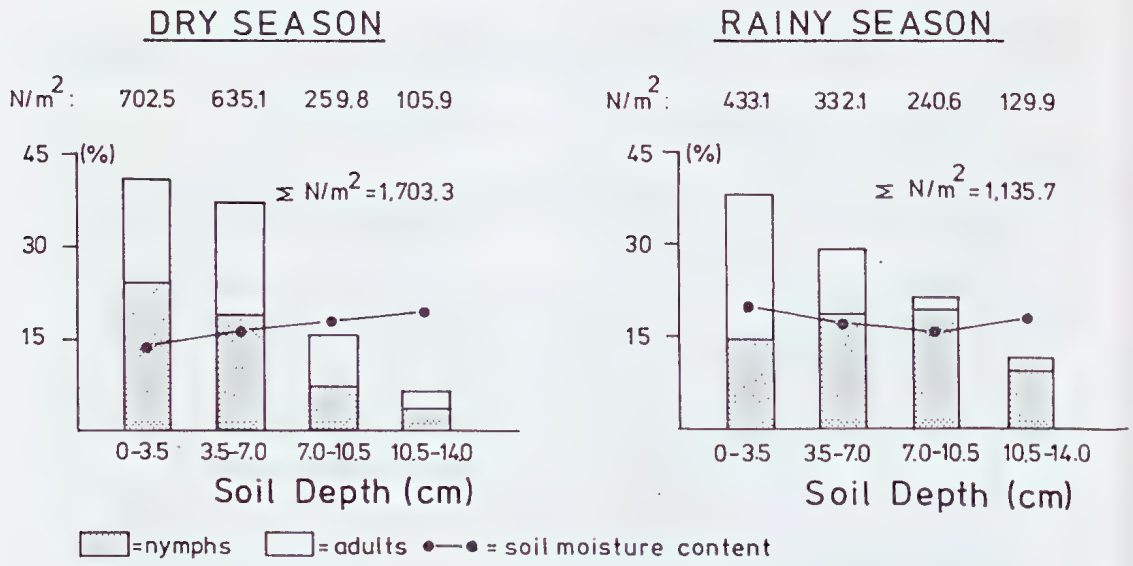

FIG. 1. Distribution of pseudoscorpions in soil and soil moisture content (both in %). Samples taken every 3.5cm to depth of 14cm in dry season and in rainy season in primary dryland forest on yellow latosol near Manaus, Brazil. Total catch each season = 100%. Abundance for each soil layer (N/m^2) and for total catch/ season ($\Sigma N/m^2$).

and on white sand soil (Adis *et al.*, 1989a, b, unpublished data; Morais, 1985). However, results were based mainly on data for orders. Evaluation of sampling data at the species level is now possible for pseudoscorpions, since identification has been completed by the second author.

STUDY AREAS

Primary Forest on Yellow Latosol

Sampling was carried out during the rainy (March) and dry seasons (October) of 1987 in a dryland terra firme forest at the Ducke Forest Reserve (= Reserva Florestal A. Ducke, 2°55'S, 59°59'W) of the National Institute for Amazonian Research (INPA, Manaus), situated on the Manaus-Itacoatiara highway (AM-010; cf. Penny and Arias, 1982). The area sampled was classified as high terra firme forest (Takeuchi, 1961; cf. Brinkmann, 1971) with several species of large, broad-trunked trees (with or without buttresses). The trees reached 44m in height (average height: 22m) and formed a closed canopy. Approximately 235 species, representing 43 families of trees, were recorded in the study area. Most frequent were Leguminosae, Rosaceae, Lauraceae, Sapotaceae and Lecitidaceae. The forest had a patchy understorey and a scanty herb layer. Guillaumet (1987), Lechthaler (1956), Prance (1990), Prance *et al.* (1976) and Rodrigues (1967) provide detailed botanical descriptions of the forest. Microclimatic data are given by Decico *et al.* (1977), Marques *et al.* (1981) and Ribeiro and Nova (1979). The soils near the Ducke Forest Reserve were described by Falesi and Silva (1969) as deep, yellow latosols, strongly weathered, excessively to very strongly acidic, of heavy texture in all profiles (A-C: 0-110cm) and with clay content of the B horizon varying from 50-70%. In the study area, where entomological long-term investigations have previously been undertaken (Adis and Schubart, 1984; Morais, 1985; Penny and Arias, 1982), the soil carried a 1-3cm thick humus layer (A_o), interspersed with fine roots and a thin leaf litter, covering most of the surface. For further details on the study area see Penny and Arias, 1982.

During the 1987 rainy season, 322mm of rain were recorded in March (data from the meteorological station at Ducke Forest Reserve, provided by M. de N.G. Ribeiro at INPA, Manaus). On the day of sampling (March 20, 1987) soil moisture content (= weight difference between wet and dried soil samples in%) was 20.0% at 0-3.5cm (= humus layer), 17.5% at 3.5-7cm, 15.5% at 7-10.5cm and 17.7% at 10.5-14cm soil depth, respectively (= mineral subsoil) (Fig. 1). Soil temperature at 10 a.m. decreased from 25.2°C in the top 3.5cm to 24.5°C at a soil

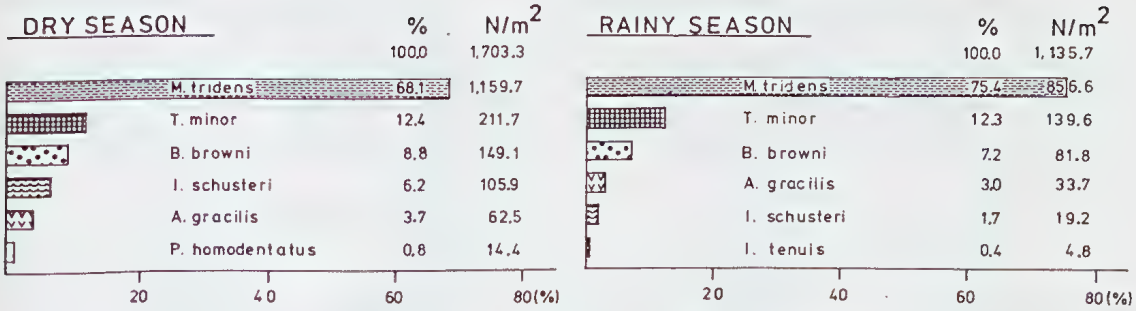

FIG. 2. Dominance (%)and abundance (N/m^2) of species of pseudoscorpions extracted from 1m^2 of soil (0-14cm depth) during dry season (October 1987) and rainy season (March 1987) in primary dryland forest on yellow latosol near Manaus, Brazil. Total catch of each season = 100%. (See text for further explanation).

depth of 14cm. The soil pH increased from 3.3 in the top 3.5cm to 3.8 in the lower layers (3.5.-14cm). During the 1987 dry season, 139mm of rain were recorded in October (data from the meteorological station at Ducke Forest Reserve). On the day of sampling (October 14, 1987) soil moisture content increased from 13.6% in the top 3.5cm to 19.1% at a soil depth of 14cm (Fig. 1) and the soil pH increased from 3.3 to 3.8. Soil temperature at 11 a.m. varied slightly (24.6-24.7°C) from the surface to 14cm.

Primary Forest on White Sand Soil

Sampling was carried out during the rainy season (March) and the dry season (August) of 1988 in a dryland campinarana forest of the Biological Reserve INPA/SUFRAMA (approx. 2°30'S, 60°10'W), at km 45 (formerly km 62) on the Manaus Boa Vista highway (BR -174). Campinarana (= caatinga arbórea) was classified as a low, relatively light forest on white sand soil with thin-stemmed trees 10-20m high, with occasional large, broad-trunked individuals, with or without buttresses, a patchy understorey and no herb layer (Guillaumet, 1987; Anderson, 1981; Lisbõa, 1975). Data on geomorphology and soil genesis are found in Chauvel *et al.* (1987). Floral inventories have been given by Lisbõa (1975), Braga (1979), Anderson *et al.* (1975), Anderson (1981) and Guillaumet (1987), while the microclimatic data were provided by Ribeiro and Santos (1975). In the study area, the white sand soil carried a humus layer that was 10-11cm thick (A_o), penetrated by a matting of roots and a thin, surface-covering leaf litter.

During the 1988 rainy season, 293mm of rain were recorded in February and 280mm in March (data from the meteorological station of EMBRAPA/UEPAE, km 54). On the day of sampling (March 18, 1988) soil moisture content (= weight difference between wet and dried soil samples in %) increased from 20.1% in the top 3.5cm to 26.2% at 10.5cm depth (= humus layer) and dropped to 9.9% at 10.5-14cm (= white sand soil) (Fig. 4). Soil temperature at 11 a.m. decreased from 24.7°C in the top 3.5cm to 24.5°C at a soil depth of 14cm. The pH of the soil was 3.2 (0-3.5cm), 3.3 (3.5-7cm), 3.6 (7-10.5cm) and 3.7 (10.5-14cm), respectively. During the 1988 dry season, 77mm of rainfall were recorded in August (data from the meteorological station of EMBRAPA/UEPAE, km 54). On the day of sampling (August 05, 1988) soil moisture content decreased from 21.9% in the top 3.5cm to 9.5% at 10.5cm depth (= humus layer) and to 9.3% at 10.5-14cm (= white sand soil; Fig. 4). Soil temperature at 3 p.m. decreased from 27.1°C in the top 3.5cm to 25.5°C at a soil depth of 14cm. The pH of the soil was 3.6 (0-3.5cm), 3.5 (3.5-7cm), 3.5 (7-10.5cm) and 3.6 (10.5-14cm), respectively. The relative light intensity on the forest floor was about 2.1% (210 lx; comparative value in the open air at 3 p.m., 10.000 lx (overcast sky); cf. Brinkmann, 1970, 1971).

METHODOLOGY

In both study areas, six soil samples were taken along a transect at random intervals with a split corer (a steel cylinder with lateral hinges; diameter 21cm, length 33cm) which was driven into the soil with a mallet. Each sample was taken to a depth of 14cm and was then divided into four subsamples of 3.5cm each. Animals were extracted from subsamples following a modified method of Kempson (Adis, 1987). All pseudoscorpions were separated by species [adults (males and females), nymphal instars] and their

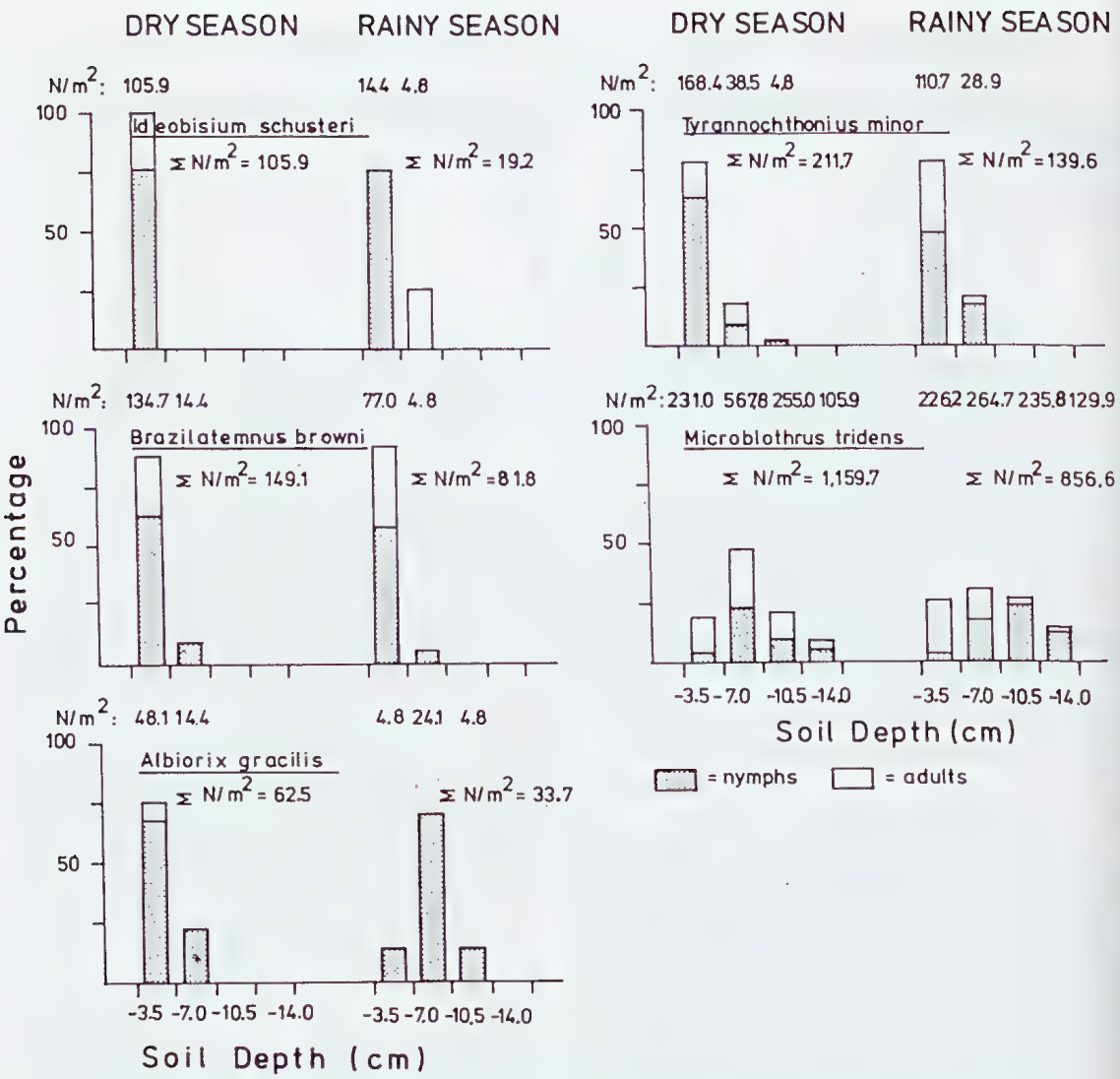

FIG. 3. Vertical distribution of five species of pseudoscorpions in soil (%). Samples taken every 3.5cm to depth of 14cm during dry season and rainy season in primary dryland forest on yellow latosol near Manaus, Brazil. Total catch each season = 100%. Abundance for each layer (N/m^2) and total catch per season (Σ N/m^2).

abundance was calculated for 1 m^2. Vertical distribution of adults and nymphs in relation to changing conditions of soil moisture content, temperature and pH was statistically evaluated with the linear correlation test (Cavalli-Sforza, 1972), using the original field data.

RESULTS

Primary Forest on Yellow Latosol

Pseudoscorpions accounted for 10-15% of all arthropods extracted from 1m^2 soil of 14cm depth (10,000-12,000 ind./m^2, Acari and Collembola disregarded) in the study area (Adis *et al.*, unpublished data). During the dry season, about 41% of all 1,700 ($\pm$71) pseudoscorpions were collected from the top 3.5.cm, 37% from below the humus layer (3.5-7cm) and 22% at 7-14cm depth. About 54% of all specimens collected represented juvenile stages (Fig. 1: nymphs). Decreasing abundance of pseudoscorpions at greater soil depths was significantly correlated with increasing soil moisture content (adults and nymphs: $P<0.01$, $r = -0.998$, nymphs only: $P<0.05$, $r = -0.956$; $n = 4$). During the rainy season, vertical distribution was similar (Fig. 1):

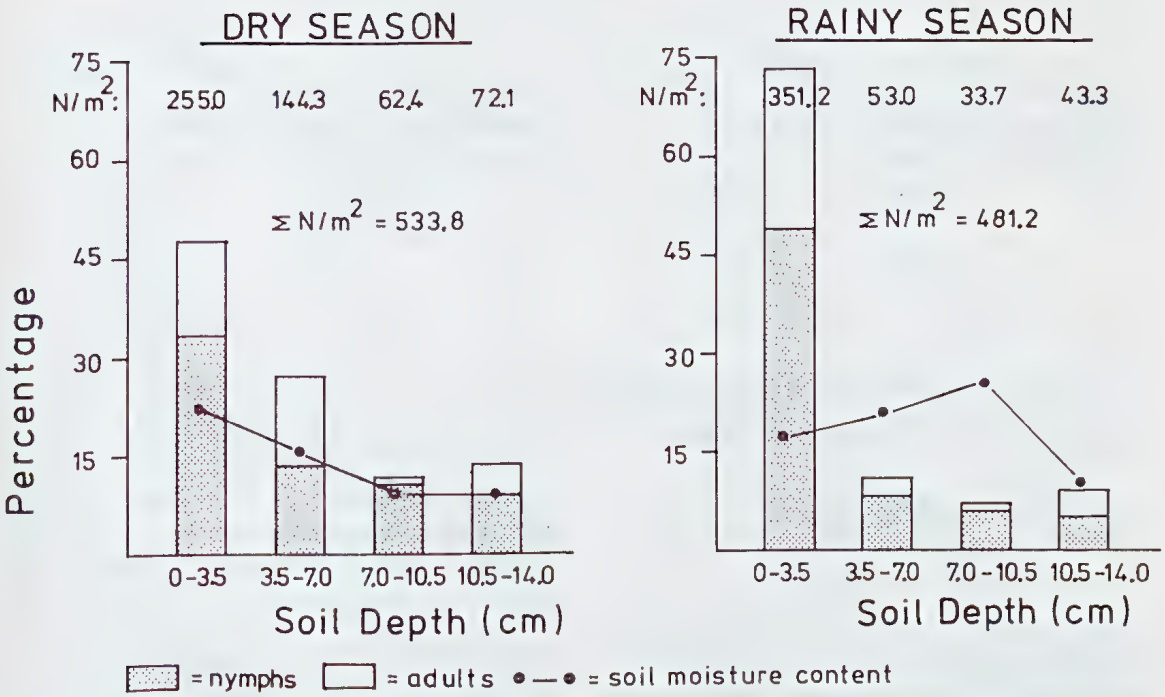

FIG. 4. Distribution of pseudoscorpions in soil and soil moisture content (both in %). Samples taken every 3.5cm to depth of 14cm during dry season and rainy season in primary dryland forest on white sand soil near Manaus, Brazil. Total catch each season = 100%. Abundance for each soil layer (N/m^2) and total catch / season ($\Sigma N/m^2$).

38% of the 1,100 (±46) pseudoscorpions were recovered from the top 3.5 cm, 29% from 3.5-7cm and 33% from 7-14cm soil depth. About 61% of the total catch were nymphs. Decreasing abundance of pseudoscorpions at greater soil depths was significantly correlated with decreasing soil temperature (adults and nymphs: $P<0.01$, $r = +0.993$, nymphs only: $P<0.05$, $r = +0.956$; $n = 4$).

Six species of pseudoscorpions were collected in both seasons (Fig. 2). All were previously reported from soils of Amazonian dryland forests (Mahnert and Adis, 1985). Syarinidae were most abundant, with *Microblothrus tridens* Mahnert (dry season: 1160±55 ind./m^2, rainy season: 860±24 ind./m^2), *Ideobisium schusteri* Mahnert and *Ideoblothrus tenuis* Mahnert accounting for 74-78% of the total catch (Fig. 2). Chthoniidae was the next most abundant family, with *Tyrannochthonius (T.) minor* Mahnert (= *Lagynochthonius minor* (Mahnert)); dry season: 212±17.4 ind./m^2, rainy season: 140±14 ind./m^2) and (dry season only) *Pseudochthonius homodentatus* Chamberlin representing 12-13% of the total catch. Less abundant (>10%) were Miratemnidae (*Brazilatemnus browni* Muchmore[1]; dry season: 149±20 ind./m^2, rainy season: 82±13 ind./m^2) and Ideoroncidae (*Albiorix gracilis* Mahnert). Few differences in dominance were found for species captured during both seasons, however their abundance varied (Fig. 2).

Except for *A. gracilis*, vertical distribution of pseudoscorpions in the soil differed between species but not within species when comparing different seasons (Fig. 3). *I. schusteri* and *B. browni* were only found at 0-7cm soil depth, with abundances being greatest in the top 3.5cm. This is also true for *T. minor* which lived, like *A. gracilis*, to a soil depth of 10.5cm. However, occurrence was restricted to the upper 7cm in *T. minor* during the rainy season and in *A. gracilis* during the dry season (Fig. 3). *I. tenuis* was found only at a soil depth of 3.5-7cm (= below the humus layer) during both seasons, whereas *M. tridens* occurred in all soil layers (0-14cm). During the dry season, significant correlation was observed between decreasing abundance of *T. minor* and greater soil depths (Fig. 3) and the

[1] At this locality, *B. browni* is apparently smaller. It may have adapted to its environment, thus representing an eco-species.

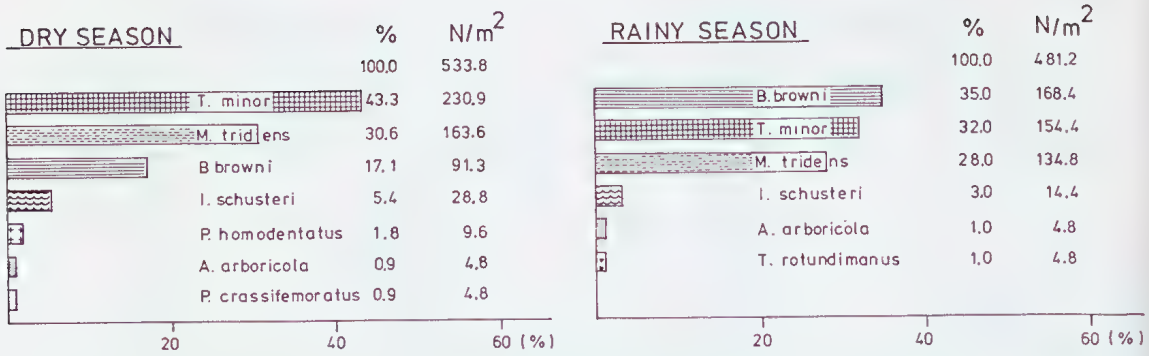

FIG. 5. Dominance (%) and abundance (N/m^2) of species of pseudo scorpions extracted from 1m^2 soil (0-14cm depth) during dry (August 1988) and rainy (March 1988) seasons in primary dryland forest on white sand soil near Manaus, Brazil. Total catch of each season = 100%. (See text for further explanation).

increased soil moisture content ($P<0.05$; adults and nymphs: $r = -0.959$, adults only: $r = -0.968$; $P<0.10$; $r = -0.936$ for nymphs only; $n=4$, respectively). Similar results were recorded from *A. gracilis* ($P<0.05$; adults and nymphs: $r = -0.969$, nymphs only: $r = +0.974$; $n = 4$). During the rainy season, decreasing abundance of *T. minor* and *B. browni* (Fig. 3) was significantly correlated with increasing pH values at greater soil depths (*T. minor*: $P<0.05$, $r = -0.970$ for adults and nymphs, $r = -0.951$ for nymphs only and $P<0.01$, $r = -0.994$ for adults only; *B. browni*: $P<0.01$, $r = -0.998$ for adults and nymphs and $r = -0.995$ for nymphs only; $n = 4$, respectively). In *M. tridens*, the increasing abundance of nymphs at greater soil depths was significantly correlated with decreasing soil moisture content ($P<0.05$, $r = -0.977$; $n = 4$). The decrease in abundance of adults, however, was significantly correlated with the decrease of the soil temperature at greater soil depths ($P<0.05$, $r = +0.962$; $n = 4$). This was also observed for nymphs of *T. minor* ($P<0.05$, $r = +0.951$; $n = 4$). Neoteny and potential parthenogenesis were confirmed for *M. tridens*, with sexually mature tritonymphs (= males) being absent (cf. Adis and Mahnert, 1990a; Mahnert, 1985).

Primary Forest on White Sand Soil

Pseudoscorpions accounted for 3-4% of all arthropods extracted from 1m^2 soil of 14cm depth (14,000-15,000 ind./m^2, Acari and Collembola disregarded) in the study area (Adis *et al.*, 1989a, b). During the dry season, about 48% of the total 530 (± 22) pseudoscorpions were collected from the top 3.5cm, 27% from 3.5-7cm, 12% from 7-10.5cm (= humus layer) and 13% from the white sand soil layer (10.5-14cm). About 66% of all specimens collected represented juvenile stages (Fig. 4: nymphs). Decreasing abundance of pseudoscorpions at greater soil depths was significantly correlated with decreasing soil moisture content ($P<0.05$; adults and nymphs: $r = +0.965$, adults only: $r = +0.952$; $n=4$) and decreasing soil temperature ($P<0.05$; adults and nymphs: $r = +0.967$; $n=4$). During the rainy season, vertical distribution was similar but more pronounced (Fig. 4): 73% of the 480 (± 27) pseudoscorpions were taken from the top 3.5cm, 11% from 3.5-7cm, 7% from 7-10.5cm and 9% from the white sand soil layer (10.5-14cm). About 68% of the total catch were nymphs. No significant correlation was found between the vertical distribution of pseudoscorpions and changing conditions of soil moisture content, soil temperature and pH.

Seven species of pseudoscorpions were obtained during the dry and six species during the rainy season (Fig. 5). All were previously reported from soils of Amazonian dryland forests (Mahnert and Adis, 1985). Chthoniidae were most abundant, with *Tyrannochthonius (T.) minor* Mahnert (dry season: 231 ± 13 ind./m^2, rainy season: 154 ± 15 ind./m^2), *T. (T.) rotundimanus* Mahnert and *Pseudochthonius homodentatus* Chamberlin accounting for 33-45% of the total catch (Fig. 5). Syarinidae was the next most abundant family with *Microblothrus tridens* Mahnert (dry season: 164 ± 10 ind./m^2, rainy season: 135 ± 8 ind./m^2) and *Ideobisium schusteri* Mahnert (dry season: 29 ± 3 ind./m^2, rainy season 14 ± 4 ind./m^2) accounting for 31-36% of the total catch. The Miratemnidae were represented by *Brazilatemnus browni* Muchmore (17-35%; dry season: 91 ± 6 ind./m^2, rainy season: 168 ± 16 ind./m^2). Less abundant ($\leq 1\%$)

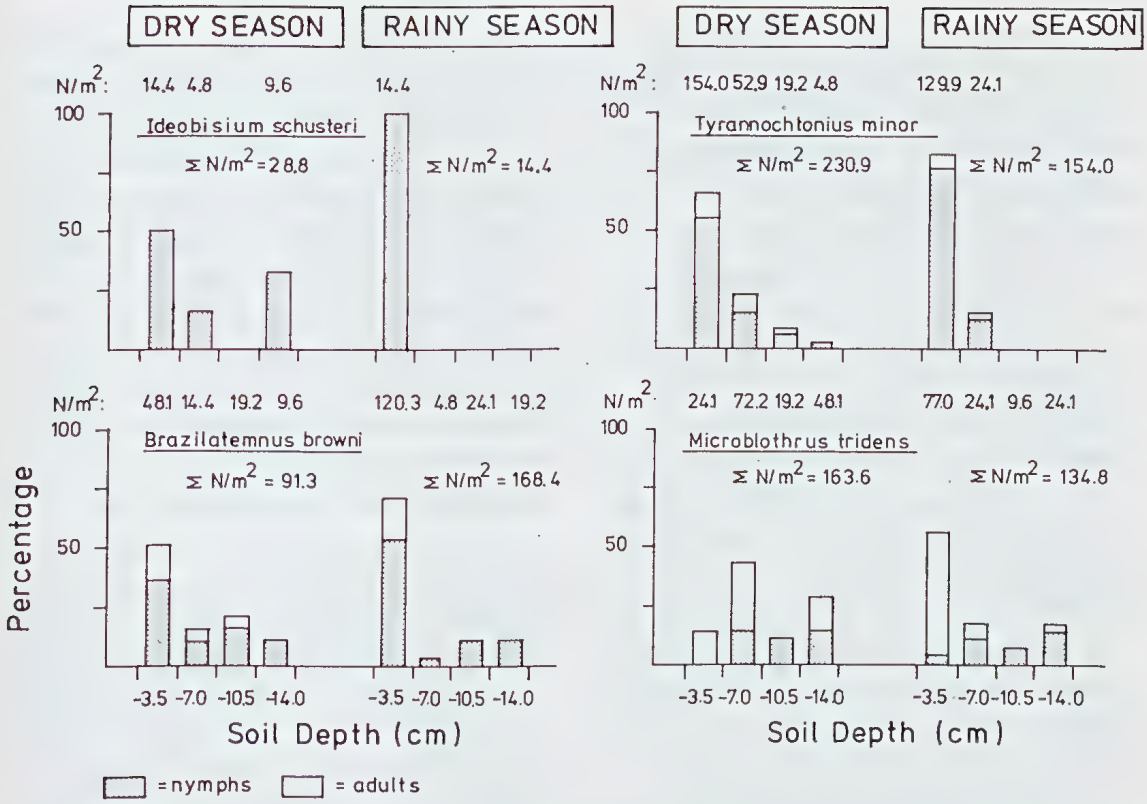

FIG. 6. Vertical distribution of four species of pseudoscorpions in soil (%). Samples taken every 3.5cm to depth of 14cm during dry and rainy seasons in primary dryland forest on white sand soil near Manaus, Brazil. Total catch of each season = 100%. Abundance given for each soil layer (N/m^2) and for total catch per season ($\Sigma N/m^2$).

were Ideoroncidae (*Albiorix gracilis* Mahnert) and Chernetidae (*Pseudopilanus crassifemoratus* Mahnert). The same four species (*T. minor*, *B. browni*, *M. tridens* and *I. schusteri*) were the most abundant in both seasons, however, their dominance in the total catch per season varied (Fig. 5). In two species, vertical distribution differed with the seasons. During the rainy season, *T. minor* and *I. schusteri* were found only from 0-7cm and in the top 3.5cm of soil, respectively. Both species were found throughout the 0-14cm soil sample during the dry season (Fig. 6). Their abundance was greatest in the top 3.5cm, independent of seasons. This is also true for *B. browni* which, together with *M. tridens*, occurred throughout the 0-14cm soil sample during the dry season as well as the rainy season. Adults of *M. tridens* were somewhat more abundant in the top 7cm, whereas no adults of *I. schusteri* were collected, probably due to low catch numbers. *A. arboricola* was restricted to the top 3.5cm. During the dry season, significant correlation between abundance and soil conditions was observed in *T. minor*: its abundance decreased at greater soil depths as the soil moisture content ($P<0.05$, $r = +0.979$ only for adults; $P<0.10$, $r = +0.935$ for adults and nymphs, $r = +0.900$ for nymphs only; $n = 4$, respectively) and the soil temperature decreased ($P<0.05$, $r = +0.967$ for adults and nymphs, $r = +0.972$ for adults; $P<0.10$, $r = +0.939$ for nymphs only; $n = 4$, respectively). No significant correlation was found during the rainy season between the vertical distribution of species and the abiotic factors investigated. In *M. tridens* sexually mature tritonymphs (= males) were absent, which confirms neoteny and potential parthenogenesis in this species (cf. 4.1.).

DISCUSSION

In Central Amazonia the abundance of pseudoscorpions in primary and secondary dryland forests on yellow latosol accounted (independently of seasons) for 3-5% of all arthropods

extracted from $1m^2$ soil of 14cm depth and for 10-15% when Acari and Collembola were excluded (cf. Adis *et al.*, 1987a, b, unpublished data). In the primary forest on white sand soil, their abundance was only 0.7-0.9% and 3-4%, respectively, due to large numbers of Pauropoda and Diplura (cf. Adis *et al.*, 1989a, b). About two-thirds of all pseudoscorpions recovered from the soil of the primary and secondary forest on yellow latosol (61-67% of the total catch) and about three-quarters of the primary white sand forest (75-84%) inhabited the top 7cm. No species were found to occur exclusively in the lower, mineral subsoil (e.g. in 10.5-14cm soil depth). Two species (*T. minor*, *B. browni*) were more abundant in the upper, organic layer in the three forests which were investigated (Figs 3, 6; fig. 3 in Adis and Mahnert, 1990a). *M. tridens*, *T. minor* and *B. browni* were the most abundant species, representing 89-95% of the total catch in the primary forests on yellow latosol and on white sand soil. They represented 58-74% of the total catch in the secondary forest on yellow latosol, where *I. tenuis* and *A. gracilis* were frequent as well (22-33% of the total catch; cf. Adis and Mahnert, 1990a). The similar spectrum of pseudoscorpion species in forests on yellow latosol and on white sand soil and especially the lack of endemic species in the latter forest type, confirm the geological results of Chauvel *et al.* (1987). They reported that the white sand area investigated represents the final stage of podzolisation, i.e. the transformation of clayey latosols to white sandy podzols by (long-term) weathering and leaching processes. If the white sand area were a large dried-up old riverbed, species composition would be different from the yellow latosol area (cf. Adis and Mahnert, 1990b).

Neither during the dry nor the rainy season was the abundance of pseudoscorpions in mineral subsoils higher in response to the changing moisture content in organic layers. This phenomenon has been reported in arthropods in the seasonally-dry tropical forests, where periods without precipitation occur [cf. climate diagrams for Central America (Walter and Lieth, 1960-67) and for Manaus (Worbes, 1986)]. Higher or lower abundance of (at least some) species at a distinct soil depth seems to be related to different abiotic factors. For example, the decreasing abundance of *T. minor* with soil depth during the dry season was correlated with soil moisture content in two forest types: negatively with increasing moisture content values in the primary forest on yellow latosol and positively with decreasing soil moisture in the primary forest on white sand soil (cf. 4.1, 4.2.). In addition, decreasing abundance with depth was also related to somewhat lower temperatures recorded from the lower levels of soil in the white sand forest. During the rainy season, no correlation was found between species abundance and soil moisture content in these two forest types. However, in the forest on yellow latosol there was positive correlation between decreased abundance of nymphs and lower soil temperatures and negative correlation between decreased abundance of nymphs, nymphs and adults ($P<0.05$) and increased soil pH. At greater soil depths there was an even higher statistical probability ($P<0.01$) of negative correlation between decreased abundance of adults and increased pH. Correlation between abundance and soil moisture content has not yet been reported for *T. minor* from the secondary forest on yellow latosol (Adis and Mahnert, 1990a). The more homogeneous occurrence of *M. tridens* in 0-14cm soil depth (Figs 3, 6; fig. 3 in Adis and Mahnert, 1990a) was correlated with soil moisture content as well: there was positive correlation between decreasing numbers of nymphs and soil moisture in the primary forest on yellow latosol during the rainy season and, correspondingly, negative correlation between increasing abundance of nymphs and decreasing soil moisture content at greater soil depths in the secondary forest on yellow latosol (cf. Adis and Mahnert, 1990a). In adults, however, there was a positive correlation between decreased abundance and soil moisture content (secondary forest) and between decreased abundance and lower temperatures at greater soil depths (primary forest).

These data all suggest that factors other than soil moisture content (abiotic and/or biotic ones) may as well cause the different distribution of pseudoscorpion species in the soil. A significant correlation, for example, was found between the abundance of pseudoscorpions and Collembola in the secondary forest on yellow latosol ($P<0.05$; dry season: $r = +0.969$, rainy season: $r = +0.989$; $n = 4$) and in the primary forest on white sand soil (dry season: $P<0.01$, $r = +0.991$, rainy season: $P<0.05$, $r = +0.967$; $n = 4$). This relationship has to be investigated in more detail, as springtails represent a potential food source for pseudoscorpions (cf. Jones, 1975; Ressl and Beier, 1958; Weygoldt, 1969). Thus, complementary studies should be carried out on reproduction patterns, food availability and trophic structure over a one-year period (cf. Adis *et al.*, 1988). Data also show that the number of samples taken per soil

layer (n= 6) was sufficient for a species dominance of 5% of the total catch, as standard deviation did not exceed 20%. Results indicate that terricole pseudoscorpions of primary dryland forests on white sand soil and of secondary dryland forests on yellow latosol represent the terricole species spectrum of a primary dryland forest on yellow latosol, which has been altered either by geomorphological/geochemical processes or human impact (cf. Morais, 1985; Rodrigues, 1986). Habitat preference in pseudoscorpions and the many habitat types existing in Amazonia are considered to be major reasons for the high species diversity found in neotropical pseudoscorpions (cf. Adis and Mahnert, 1985, 1990b).

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NEST ASSOCIATES OF *CLUBIONA ROBUSTA* L. KOCH (ARANEAE: CLUBIONIDAE) IN AUSTRALIA

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Austin, A.D. 1993 11 11: Nest associates of *Clubiona robusta* L. Koch (Araneae: Clubionidae) in Australia. *Memoirs of the Queensland Museum* **33**(2): 441-446. Brisbane. ISSN 0079-8835.

The nests of *Clubiona robusta*, whether or not they contain a resident female spider, are usually inhabited by other invertebrates, here termed nest associates. The abundance and diversity of nest associates for *C. robusta* are described from sampled nests. Associates recorded were: other spiders, Acarina, Mollusca and insects of the orders Collembola, Coleoptera, Heteroptera, Hymenoptera, Lepidoptera, Neuroptera, Psocoptera and Thysanoptera. The presence of a resident female was a factor which affects the abundance and diversity of associates. Biological notes on each group of nest associates are given. Results for *C. robusta* are compared with data on other spiders in the same habitat, and other categories of nest associates used in other studies.□*Araneae, Clubionidae, parasitoid, predator, eggs, spider nest.*

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Most vagabond spiders build a silken retreat in which they moult, mate, lay eggs and protect themselves and their eggs from predators and extreme environmental conditions (Jackson, 1979; Jackson and Griswold, 1979; Pollard and Jackson, 1982; Austin, 1984a, 1988; Wolf, 1990). Different species construct a great variety of retreats which vary in size, structural complexity and the location in which they are placed. For *Clubiona robusta* L. Koch, a moderate-sized clubionid (body length about 15 mm) which inhabits the corticating (shedding) bark of eucalypt trees in south-eastern Australia, two types of retreats have been recognized: flimsy, thin, silk-walled moulting chambers constructed by juveniles, and thicker walled nests constructed by mature females for egg laying (Austin, 1984a).

Whatever the structure of spider retreats, they often attract an array of other invertebrates (termed 'nest associates') which utilize them in a variety of ways (Auten, 1925; Jackson and Griswold, 1979; Griswold, 1986). This aspect of spider retreats has been examined only rarely. A study of the nest associates of the salticid *Phidippus johnsoni* Peckham and Peckham in the U.S.A. by Jackson and Griswold (1979) is the only known detailed work. Jackson and Griswold (1979) divided nest associates into eight categories, following the three described by Auten (1925), based on their biological relationship with the resident spider, its eggs or the nest itself (see Table 1). Most of these biological categories have also been recognized for two eresid species in South Africa (Griswold, 1986).

During a study of the biology of *C. robusta* in South Australia (Austin, 1984a, 1988), incidental observations showed that 1) most nests contained at least some associates, 2) associates inhabited both vacant and occupied nests, and 3) the size range of associates appeared to differ between vacant and occupied nests. This study then sets out to detail the diversity and abundance of nest associates found in *C. robusta* nests, and the factors that might determine their number and size.

MATERIALS AND METHODS

Nests of *C. robusta* were collected from under the bark of eucalypt trees with large plates of corticating bark at their bases (i.e. *Eucalyptus camaldulensis*, *E. cladocalyx*, *E. leucoxylon* and *E. viminalis*) in the Mylor area of the Adelaide Hills, South Australia (see Austin, 1984a). Nests were collected at random in the summer (December-February) over three years (1979-1981). Nests constructed only in that summer were included in samples. The whiter, fresher colour of the silk was used to distinguish them from nests built in previous seasons. Samples included vacant nests, nests containing a resident spider, and nests containing a resident spider and egg-mass or hatched juveniles. In the field, after bark plates were removed from trees, nests were gently teased away and placed in screw-top plastic vials (40 mm dia.). A large white dish prevented accidental loss of any associates or resident spiders. In the laboratory, when nest associates were en-

Category	Description
1a	Endoparasitoids of spiders that seek out and/or emerge from their hosts inside nests
1b	Ectoparasites and ectoparasitoids of spiders that seek out and/or emerge from their hosts inside nests
2	Endoparasitoids of eggs in nests
3a	Predators of eggs in nests (including 'ectoparasitoids')
3b	Predators of spiders in nests
4	Scavengers feeding on dead spiders or other material in nests
5	Predatory spiders that adopt nests as a predatory device
6	Spiders that adopt the nests of other spiders as a refuge or substitute for constructing their own nests
7	Organisms (other than spiders) that adopt nests as a refuge or pupation site
8	Accidental inhabitants
9	Conspecific males

TABLE 1. Categories of nest associates, modified after Jackson and Griswold (1979) (see text for further information).

countered, details of the nest were recorded along with any relevant biological information for the associate, and they were then preserved in 70% alcohol for identification. Parasitized spider eggs and the larvae and pupae of mantispids, pompilids, Diptera and Lepidoptera were left to emerge prior to preservation. As in Jackson and Griswold (1979), nest associates only within the nest, within the silk matrix of the nest wall, or under the nest were collected, not those completely outside or near the nest. To compare differences in the diversity, size and abundance of associates between vacant nests and those occupied by a resident female, 30 nests of each type were collected at random in the field during January 1980 and examined.

Voucher specimens of each nest associate were lodged in the Department of Crop Protection insect collection, Waite Campus, University of Adelaide, South Australia.

RESULTS

Over 400 nests sampled during the summers of 1979 to 1981, yielded over 40 species of nest associates including Acarina, Araneae, Collembola, Coleoptera, Diptera, Heteroptera, Hymenoptera, Lepidoptera, Neuroptera, Psocoptera, Thysanoptera and Mollusca (Table 2). The biological association of each associate with *C. robusta* (categories listed in Table 1), whether determined by direct observation or only assumed, is also given for each species in Table 2. The exact category of individual associates could be assigned only for those species whose biology was observed directly (e.g., parasitoids or predators of eggs or adult *C. robusta*–?*Ogcodes* sp., *Ceratobaeus masneri* Austin), or for those species whose biology was well enough known to rule out all categories except one (e.g., Lepidoptera pupating in nests or Hymenoptera which specifically parasitize other spiders). For other associates, multiple categories are listed to indicate the range of biological associations that might exist. For many species it was impossible to determine whether nests were being used as a specific refuge or the species was there by accident (categories 7/8). For others, their association with *C. robusta* appeared to vary. Gnaphosid and segestriid spiders were observed in the field preying on subadult *C. robusta* (category 3b, see below), as well as constructing their own nests inside those of the host spider (category 6).

Nest associates seemed to occur both in vacant nests and those occupied by a female spider, there appearing to be fewer and smaller associates in the latter. To test these hypotheses, i.e. that occupied nests had fewer and smaller associates, the fauna from 30 occupied nests and 30 vacant nests were compared (Table 3). Of the 40 recognized taxa that were collected during the 1979-81 survey, 28 were found in the 60 sampled nests, with Diptera and Neuroptera being the ordinal taxa not recorded. The 30 occupied nests had substantially fewer nest associates (total 147) compared with vacant nests (227) (see Table 3). Using a Wilcoxin test (Zar, 1984) occupied nests contained significantly fewer associates per nest than vacant nests ($Z = 2.36$, $P < 0.02$), and significantly fewer associates larger than 2.5 mm in length ($Z = -4.38$, $P < 0.0001$). The two major groups of associates that seemed to differ most notably between vacant and occupied nests were other species of spiders and Coleoptera, which were both mostly represented by individuals much greater than 2.5 mm long. This specific size was chosen to test for differences in size of nest associates because previous work on *C. robusta* has shown that this is about the minimum size for potential prey that females spiders can physically handle (Austin, 1988). Hence, one suggested cause for fewer large associates in occupied nests is that they would be killed or driven away by the resident spider.

Biology of Nest Associates

Assigning nest associates to one or more biological categories first required that those used by Jackson and Griswold (1979) be modified. In particular, endo- and ectoparasitoids have been

Taxonomy of nest associate	Associate Category	*C. robusta* I	II	III
Acarina: Mesostigmata				
Phytoseiidae *Seiulus* sp.	4/7/8	+	5	2
Acarina: Prostigmata				
Bdellidae *Bdellodes harpax* (Atyeo)	4/7/8	+	2	2
Cyta latirostris (Hermann)	4/7/8	+	1	1
Anystidae genus & sp. indet.	4/7/8	+	6	7
?Eupalopsellidae genus & sp. indet	4/7/8	+	1	2
Erythraeidae genus & sp. indet	4/7/8	+	3	2
Araneae				
Clubionidae *Clubiona cycladata* Simon	3a/6/8	+	3	2
C.robusta L.Koch ♂	9	+	8	2
Clubiona spp. juveniles*	6/8	+	16	11
Gnaphosidae *Intruda* sp.	3a/3b/6/8	+	2	0
Hahniidae *Scotospilus* sp.	3a/6/8	+	0	0
Lamponidae *Lampona* sp.	3a/3b/6 /8	+	1	0
Salticidae *Myrmarachne* sp.	3a/6/8	+	3	0
Servaea sp.	3a/6/8	+	1	0
Segestriidae *Ariadna* sp.	3a/3b/6 /8	+	2	0
Collembola				
Entomobryidae *Drepanura* sp. 1 & 2*	4/7/8	+	11	7
Neanuridae *Setanodosa* sp.	4/7/8	+	5	3
Coleoptera				
Coccinellidae *Scymus parallelus* Blackburn	4/7/8	+	5	2
Dermestidae *Anthrenus* sp.	4/7/8	+	2	1
Trogoderma antipodum Blackburn	4/7/8	+	1	0
Tenebrionidae genus & spp. indet.*	4/7/8	+	11	6
Diptera				
Acroceridae ? *Ogcodes* sp.	1a	+	0	0
Chloropidae *Pseudogaurax* sp.	3a	+	0	0
Heteroptera				
Reduviidae *Empicoris rubromaculatus* (Blackburn)	3a/7/8	+	4	2
Pentatomidae *Nezara viridula* L.	7/8	+	0	0
Poecilometis sp.	7/8	+	0	0
Hymenoptera				
Eulophidae *Tetrastichus* sp.	3a	+	0	0
Formicidae *Iridomyrmex* sp.	3a	+	3	0
Scelionidae *Ceratobaeus clubionus* Austin	7/8	+	2	2
C. lamponae (Hickman)	7/8	+	0	0
C. masneri Austin	2	+	4	7
Gryon sp.	7/8	-	1	0
Trissolcus sp.	7/8	-	0	1
Pompilidae *Epipompilus* sp.	3a	+	0	0
Lepidoptera				
Limacodidae *Doratifera* sp. (pupa)	7	-	1	0
genus & spp. indet. (larvae)*	7/8	+	0	0
Neuroptera				
Mantispidae *Austromantispa* sp.	1b/3a	+	0	0
genus & sp. indet. (larva)	1b/3a	+	0	0
Psocoptera				
Lepidopsocidae genus & spp. indet.*	4/7/8	+	2	5
Liposcelidae *Liposcelis* sp.	4/7/8	+	6	8
Thysanoptera Thripidae genus & spp. indet.*	4/7/8	+	6	7
Mollusca: Gastropoda Helicidae *Cochlicella ventrosa* (Ferussac)	4/7/8	+	1	0

TABLE 2. Nest associates in nests of *Clubiona robusta* and category of associate to which they belong (see Table 1 and text). I = associates found at least once (+) in occupied or vacant nests over three-year period (1979-81); II = no. of nests in which each associate occurred in sample of 30 vacant nests (Jan 1980); III = no. of nests in which each associate occurred in sample of 30 nests occupied by ♀ spiders (Jan 1980); * = nest associate represented by more than one species.

distinguished (categories 1a and 1b), and predators of spiders and their eggs divided into separate categories (3a and 3b). The term 'parasitoid' (Askew, 1971) is used for species that kill their host (e.g., scelionid egg parasitoids), and 'parasite' for species that feed from but normally do not kill their host (e.g., mantispid larvae feeding on adult spiders, see below). 'Ectoparasitoids' of eggs, a term used by some authors, are not distinguished from egg predators (Austin, 1985; LaSalle, 1990). Also, a new category has been added; that of conspecific males (category 9, see below).

Notes on the biology of nest associates were made both in the field and on nests and associates kept for short periods in the laboratory, during the three-year survey of nests.

Scavengers, refuge seekers and accidental inhabitants. Most nest associates belong to one of these categories (25/40 taxa), but without detailed biological studies on individual species, it was impossible to determine in which specific category they belonged. The major groups are Acarina, Collembola, Coleoptera, Pentatomidae (Heteroptera), Lepidoptera, Psocoptera (New, 1974), Thysanoptera and Mollusca. In addition, three parasitic wasps can be categorized as either refuge seekers or accidental inhabitants; *Ceratobaeus clubionus* Austin, an egg parasitoid of other clubionid spiders (not *C. robusta* -Austin, 1984b), *Ceratobaeus lamponae* (Hickman), an egg parasitoid of *Lampona* spp. (Hickman, 1967a), and *Trissolcus* sp. and *Gryon* sp., egg

Statistics	Nest residents	
	no ♀	resident ♀
No. of nests sampled	30	30
Total no. of associates	227	147
Mean no. of associates/nest	7.63	4.90
Total no. of associates >2.5mm	72	13
% of associates>2.5 mm	31.7	8.9
Mean no. of associates/nest> 2.5mm	2.33	0.47

TABLE 3. No. of nest associates for vacant nests and nests occupied by resident ♀ spider.

parasitoids of pentatomid bug eggs (Masner, 1976).

Other spiders that use C. robusta nests. More than 50% of vacated nests were occupied by other spiders, including conspecifics, many of which had constructed moulting retreats or their own nests inside that of *C. robusta* (category 6). Sixteen of 30 vacant nests contained juvenile *Clubiona* which, in most cases, could not be identified to species. Some of these may have come from previously hatched eggmasses in the same nest. However, 11 of 30 occupied nests also contained *Clubiona* juveniles, 8 of which contained gravid female *C. robusta* and no previously hatched eggmasses, indicating that these juveniles had migrated from other nests. Ten out of 60 nests sampled in January 1980 contained conspecific adult males, two cohabitating with mature females and eight found in older, vacated nests. Other spiders were encountered more rarely in the survey and only in vacant nests. All species, except for the hahniid *Scotospilus* sp. and the segestriid *Ariadna* sp., at least once constructed retreats or nests inside nests of *C. robusta*.

Parasitoids and parasites of adult C. robusta. Only on two occasions were such organisms recorded. One acrocerid fly (?*Ogcodes* sp.) was reared from a female *C. robusta* (category 1a) (Schlinger, 1987) and a single mantispid larva (possibly *Austromantispa* sp.) was found attached to the pedicel of a gravid female inside a nest (category 1b). Some mantispids are now known to act as ectoparasites of female spiders as small larvae and then as predators of the eggs as larger larvae (Redborg, 1982; Redborg and Macleod, 1983).

Predators of adult C. robusta. The only potential predators of adult *C. robusta* collected during the study were other large spiders, but no such predation was noted (category 3b). Four cases of predation on subadult *C. robusta* outside of retreats were recorded, two each by *Intruda* sp. and *Ariadna* sp. Also, no spider were noted using *C. robusta* nests as a predatory device (category 5, see Jackson, 1976; Jackson and Griswold, 1979).

Parasitoids and predators of C. robusta eggs. An endoparasitic wasp, *Ce. masneri*, was the most commonly noted species (category 2) and was associated with vacant nests, occupied nests without eggmasses, and occupied nests with eggmasses. This wasp caused the highest level of egg mortality (22-25%, Austin, 1984b, 1988) of all species found feeding on eggs. Four species thought to be specific predators ('ectoparasites' of other authors) were seen feeding on *C. robusta* eggmasses only rarely (category 3a). These included a chloropid fly, *Pseudogaurax* sp., on three occasions (Austin, 1985), a eulophid wasp, *Tetrastichus* sp. (LaSalle, 1990), a pompilid wasp, *Epipompilus* sp. (Pollard, 1982), each on one occasion, and a mantispid, *Austromantispa* sp., on two occasions. The only generalist predator of eggs recorded was the ant *Iridomyrmex* sp. which was observed feeding on eggmasses and hatched eggs several times, but only in vacant nests (Austin, 1988). Other possible predators of eggs include a reduviid, *Empicoris rubromaculatus* Blackburn, and other spiders.

Nest Associates of Other Spiders on Eucalypt Bark

During the 1979-81 survey, while collecting nests of *C. robusta*, nests of three relatively common spiders were also collected and their nest associates examined. Observations on these three species are presented here. Other species were either too rarely encountered to report on here or were not found associated with their nests.

Servaea sp. (Salticidae). This same species (or one very similar) was figured as *Plexippus validus* Urquhart by Hickman (1967b), who described some aspects of its biology in Tasmania. The spider constructs a flattened, circular nest (30-40 mm dia.) of dense, white silk, similar in appearance and density to cotton wool. Twenty-five nests were collected: 20 occupied by female spiders, and 10 contained eggmasses or hatched juveniles. Only six associates were identified from these nests: *Austromantispa* sp. 2 (two nests), *Ogcodes* sp. (one nest), *Pseudogaurax* sp. 2 (seven nests), *Iridomyrmex* sp. (one nest), *Anthrenus* sp. (one nest) and an unidentified carabid beetle (one nest). *Iridomyrmex* sp. was feeding on eggs inside a vacant nest. The *Austromantispa* sp., *Ogcodes* sp. and *Pseudogaurax* sp. in these nests were different from those in *C. robusta* nests. Mites, Collembola and

Psocoptera were seen in some nests but were not extracted and identified. No scelionid wasps were reared from eggmasses.

Breda jovialis (L. Koch) (Salticidae). This easily recognized salticid builds a disc-shaped nest (about 30 mm dia.) with two prominent tubular entrances opposite each other (Hickman, 1967b). The surface of the nest is hardened and parchment-like, but the inside is lined with dense, flocculent, white silk. Seventeen nests were collected: six had resident, gravid females, and five had females with eggmasses. Only two associates were identified, and both were feeding on eggs. These were *Idris* sp. (Scelionidae) and *Pseudogaurax* sp. Another scelionid is known to parasitize *B. jovialis* eggs elsewhere in Australia (Hickman, 1967a; Austin, 1981), but this species was not found in South Australia. As for *Servaea* sp., mites, Collembola and Psocoptera were seen in a few nests but were not extracted and identified.

Ariadna sp. (Segestriidae). This species builds a flattened oval or tubular nest with walls of similar construction and silk density to that of *B. jovialis*. Only nine nests were collected, all contained resident females, and four contained eggmasses. The only nest associates recorded were the larvae of a hymenopteran egg predator in one nest. These failed to develop and thus could not be identified. No mites, Collembola and Psocoptera were seen in the nests of this species.

DISCUSSION

The number of species of nest associates collected from *C. robusta* nests and the major taxa represented were similar to that found in nests of a salticid, *P. johnsoni* (Jackson and Griswold, 1979). However, *C. robusta* differed in that many more contained associates: of the 60 sampled nests 55 (92%) contained at least one associate, whereas only 1.2 % of *P. johnsoni* nests were occupied by associates. No nests of *P. johnsoni* occupied by a resident female spider contained associates, whereas most occupied *C. robusta* nests did (87%). *P. johnsoni* nests also differed in that a much greater proportion of recorded associates were spiders (66%), whereas for *C. robusta*, even excluding Acarina and Collembola, only 26% of associates were spiders. The reason for these differences is unclear, but is probably due to differences between the habitats of the two spiders and the size and nature of potential invertebrate faunas that exist at the two locations. Certainly, the bark of eucalypt trees examined in this study harbour a large and diverse invertebrate fauna that acts as a reservoir for *C. robusta* nests. Also, the apparent high and consistent abundance of this fauna means that there is probably a much greater chance of nests being inhabited, compared with the places *P. johnsoni* constructs nests, i.e., under rocks, pieces of wood, and in hollow reeds (Jackson, 1979).

Occupied nests of *C. robusta* have smaller nest associates compared with vacant nests presumably because resident spiders are known to kill and feed on intruders larger than 2.5mm. Also, females are known to guard their eggmasses and kill even distasteful intruders in nests (Austin, 1988). However, the aggressiveness of resident spiders does not explain why there are fewer small associates (<2.5 mm) in occupied nests (see Table 2). One possible reason for this is that the activity of female spiders in building, repairing and tidying nests, disturbs many small invertebrates and they move away.

The notes on nest associates of other spiders given here pose some questions. Generally the nests of the three species examined have structurally more complex nests than does *C. robusta*, and this is associated with them having far fewer nest associates. In the light of this association, further research on nest associates could profitably examine the structure of nests as a factor regulating the number and types of nest associates, as could differences in the behaviour of resident spiders inside their nests.

Finally, the biological categories proposed by Jackson and Griswold (1979) for the nest associates of *P. johnsoni* were directly applicable to the associates recorded here for *C. robusta* and the other three spiders examined and, thus, probably can be applied to the associates of any nest-building vagabond spider. We have modified their scheme in two points: 1) to distinguish between endo- and ectoparasitoids, because these two types of parasitoids have basically different biologies (Austin, 1985; LaSalle, 1990), and 2) to include conspecific males as a new category, which were found in both occupied and vacant nests.

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A TENTATIVE ANALYSIS OF THE SPIDER FAUNA OF SOME TROPICAL OCEANIC ISLANDS

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The spider fauna of oceanic islands in the Pacific (Galápagos, Juan Fernandez, Easter Island, Marquesas, Hawaii), the Atlantic (Saint Helena) and the Indian Ocean (Comoros, Seychelles) is analysed. Family composition, size frequency distribution, species/area relationship, the origin of the faunas and their qualitative compositions are discussed. The colonization of the islands by spiders appears to be greatly influenced by the accessibility of the island, its habitat diversity and the speciation capacity of particular groups. Most of the fauna is composed of species transported by man. Thorough analysis of island faunas is still hampered by the lack of complete published data sets.

Les faunes aranéologiques des îles océaniques situées dans le Pacifique (Galápagos, Juan Fernandez, Marquises, Hawaii) l'Atlantique (Sainte-Hélène) et l'Océan Indien (Comores, Seychelles) sont analysées. Leur composition au niveau de la famille, la distribution des fréquences de taille, leur origine et leur composition qualitative sont discutées. La colonisation des îles par les araignées semble être fortement influencée par l'accessibilité de ces îles, leur diversité en habitats et la capacité de spéciation de certains groupes. Une grande partie des faunes est composée d'espèces apportées par l'homme. Une analyse complète des îles océaniques est encore impossible à cause du manque de données complètes publiées.
□*Araneae, island zoogeography.*

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Most studies of island spiders have been confined to the description and enumeration of species. A general explanation of the composition of the araneological fauna of islands has not been tried. The availability of many almost complete species lists of remote oceanic and granitic islands allows us to analyse these spider faunas and try to understand their compositions. Only a few data-sets (those of Galápagos and Saint Helena) are nearly complete and most others are likely to grow considerably. For several islands the species lists included many unidentified species submitted for study to us or present in other collections (e.g. Cocos: Natural History Museum of Los Angeles County). Nevertheless we have tried to find patterns in the composition of the tropical island spider faunas.

MATERIAL AND METHODS

Apart from the spiders of the Galápagos and the Comoros, all data used are from the literature (Table 1). Hence, in the analysis of the size distribution, we had to use the total length, which is a less reliable measure than carapace width or the size of another sclerotised body part.

To compare the family composition, the number of species in each family was expressed as a percentage of the total number of species. The Renkonen-index was used to calculate the percentage of similarity.

RESULTS AND DISCUSSION

Family Similarity

Because the islands are in different zoogeographical provinces, a comparison of their faunas on the species level is not informative.

Similarity on family level was surprisingly high between the Galápagos, the Hawaiian Archipelago (Pacific) and Saint Helena (Atlantic), reaching ca 70% (Fig. 1). A second group (ca 60% similarity) consists of the Seychelles and Cocos Islands. These distinct vegetation belts, as on the main islands of the first group, seems important and induces a similar family composition. These islands were initially covered entirely by forest. The southern pacific Easter Island and Juan Fernandez, now covered by a gramineous, so called pampa-vegetation, have little similarity in family constitution.

Body Length Frequency Distribution

In tropical continental habitats, e.g. savanna

Island/ archipelago	Area (km^2)	Highest elevation (m)	Distance to nearest continent (km)	Age (my)	Literature Consulted
Cocos I. (CO)	46.6	849	500 (Costa Rica)		Hogue and Miller (1981)
St Helena I.(SH)	120	705	1800 (Africa)	14.3	Benoit (1977)
Easter I. (PA)	165.8	530	3760 (Chile)	2.5	Skottsberg (1920), Berland (1924)
Juan Fernandez I. (JF)	178	1500	660 (Chile)	10	Skottsberg (1954)
Seychelles Arch. (SE)	273	914	932 (Madagascar)	65	Benoit (1978a, b), Saaristo (1978)
Marquesas Arch. (MA)	1274	1200	6300 (Perú)		Berland (1935, 1939)
Galápagos Arch. (GA)	7882	1707	960 (Ecuador)	9	Jackson (1985), Baert *et al.* (1989a, b)
Hawaii Arch. (HA)	16504	4206	4000 (Mexico)	70	Suman (1964, 1965), Gertsch (1973)
Comores Arch.	2237	2300	300 (Madagascar)	1	Jocqué (1985)

TABLE 1. Summary data (age is approximate) of islands and archipelagos considered.

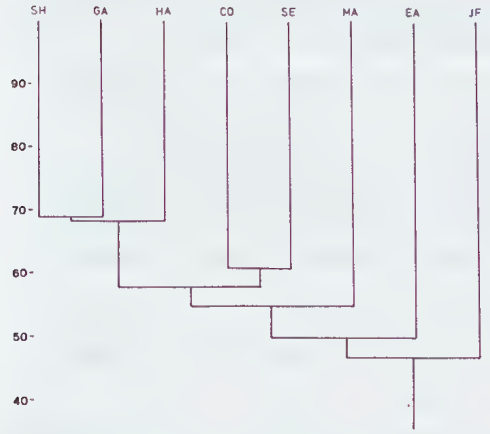


FIG. 1. Dendrogram of the similarities between the islands/archipelagos on family level.

and secondary forest in Ivory coast (Jocqué, 1980), middle-size spiders in the class of 4-6mm dominate (Fig. 2). However, data for Ivory Coast are based entirely on pitfall trap samples. That may bias the size frequency distribution towards higher or lower averages. On the other hand, the collections from islands are clearly biased towards larger spiders. Earlier collectors are more likely to have taken conspicuous large webspiders than small soil dwelling spiders. As for the other analyses it is probably too early to detect relevant differences in size distributions on different islands as compared to the situation on the continent.

Only spiders from Galápagos, Cocos Island and the Seychelles seem on average smaller than those from the collections made with pitfall traps in West Africa (Table 2). As only the difference GA-RCI is significant ($\chi^2 = 23.84$; $P < 0.02$) it seems that the discrepancies are further meaningless. However, complete data from the islands and fully comparable data from the continent might reveal more differences in average size of island and continental spiders. We expect selection to favour small spiders during the colonisation process. Thus, many more small spider species are likely to be present on islands than on the continent. Smaller spiders live in higher densities than bigger ones and the possibility that they reach an island is statistically higher than for larger spiders. Moreover, smaller spiders are usually better aeronauts although young stages of larger spiders have often been observed to balloon as well. The chance that a raft–rafting being an important mean of colonisation–contains a 'propagule' is also likely to be higher for smaller spiders than for larger ones.

However, the possibility for survival of spiders that reach an island is probably better for larger than for smaller ones but the enormous differences in specific ecophysiological characters make it difficult to generalise.

The Seychelles are granitic continental fragments and must have had a well-balanced fauna when they separated from the mainland. Hence, they should have elements of a continental spider fauna. Apparently this is not so. Some unusually large soil-dwelling spiders do exist on the island (see below), but the smallest size class seem more important on that archipelago, just as on the others. The Seychelles are a group of small islands with the largest not exceeding $15km^2$. When ocean levels were higher these islands must have been tiny and the chance for extinction very high. Larger spiders occur in smaller populations. Thus, they are more liable to become extinct hence the otherwise unexpected dominance

TABLE 2. Mean body length (mm), number of species and standard deviation (RCI = Ivory Coast).

	SH	SE	PA	CO	GA	JF	MA	HA	RCI
$\bar{x}$	6.75	5.57	6.45	4.79	5.52	7.63	6.40	6.82	5.82
n	95	125	22	29	136	31	41	127	134
SD	4.47	4.62	3.47	4.20	4.23	5.58	3.35	3.98	3.91

of smaller spiders on the Seychelles. The spider fauna of Seychelles is probably too little known because the two main expeditions (Benoit 1978, Saaristo 1978) were in the dry season.

Frequency distribution histograms for the smaller Pacific islands (Easter, Juan Fernandez and Cocos) and for the Marquesas archipelago, show very irregular shapes. The distribution seems to have several peaks.

There may be several reasons for this:

1 the fragmentary knowledge of their spider fauna. Few spider species are listed for these islands in the literature. Occasional samples, made by other zoologists during brief visits to Easter Island, yielded important new records of spider species. That is apparently true of our knowledge of the spider fauna of most tropical islands.

2 Cocos and Easter Island are still too young or are so isolated (Easter Island in the centre of the South Pacific Gyre; Juan Fernandez amidst the northerly directed Humboldt Current) that they are difficult to colonise and an equilibrium in their spider communities has not yet been reached.

3 due to their limited size and low habitat diversity these islands cannot support more species and do indeed have several size distribution peaks.

Relation between Island Area and Species Density

Tropical African oceanic islands are far richer in species and their species/area relationship is much higher (0.48-0.81) than for tropical Pacific oceanic islands (Table 3). The very small Cocos Island lying the closest to a continental landmass is exceptional in this respect (0.60). Tropical Pacific archipelagos (0.01-0.04) and the southern pacific islands (0.14-0.18) have relatively low species/area relationships. It is not clear why the African off-shore islands are so much richer than the others. The source areas may be richer but that must be proven by thorough studies of the continental spider faunas. Many more species may have been introduced on the African islands. This is probably true for Saint Helena that has an unusual large proportion (44%) of introduced spiders, mainly from temperate regions. It is doubtful whether that is a sufficient explanation.

There is a relationship between altitude (highest elevation) of the island and the number of species present (Fig. 3.1: $r = 0.677$, $p > 0.01$) and between area of the island and the number of species present (Fig. 3.2: $r = 0.716$, $p > 0.001$). In both cases there is a significant correlation.

Origin of Faunas

As the distance from an island from the mainland increases, its component of continental species decreases.

Very striking is the much lower percentage of continental species on the African islands as compared to those of the Pacific. The same is true for the southern Pacific islands Juan Fernandez and Easter Island. This could be explained by their isolated position. Juan Fernandez lies in the middle of the northerly directed Humboldt Current, whereas Easter Island is situated a long distance from the continent in the centre of the South Pacific Gyre, making the arrival by rafting rather unlikely.

The presence on the Galápagos islands of northern, central (with Antillean elements), as well as southern American elements, could be explained by their special situation astride the equator. The archipelago lies in such a position that it is reached by the warm Niño Current in the rainy season and by the cold Humboldt Current in the dry season. The Californian Current of the Northern Hemisphere runs southwards along the North American coast and reaches the Panama Basin where it is warmed up and turns towards the Galápagos as the Niño Current. The southern Humboldt Current runs northwards along the south American coast and turns westward near the equator towards the Galápagos. Rafts can easily be transported from the north as well as from the south. A floating raft takes about two to four weeks to reach the islands from the South American mainland (Schatz, 1991).

Furthermore, there was a broad connection between the Caribbean region and the eastern Pacific area from 48 my until 3.5 -3 my ago (Woodring, 1959; Jones and Hasson, 1965) with a sea current running from the Atlantic to the Pacific (Petuch,1982). The Panama isthmus was plugged some 3 my ago by the Caribbean Plate which was shoved in between the north and south American plates. At that time the Galápagos islands had already emerged from the sea. It is acceptable that many fauna elements of the Caribbean reached the Galápagos at that time. Nearly 82% of the known spider species of Cocos Island are continental species.

The Marquesas have more species of Pacific origin. This can be expected because of the position of this archipelago at the margin of the Polynesian province (NE end of the south

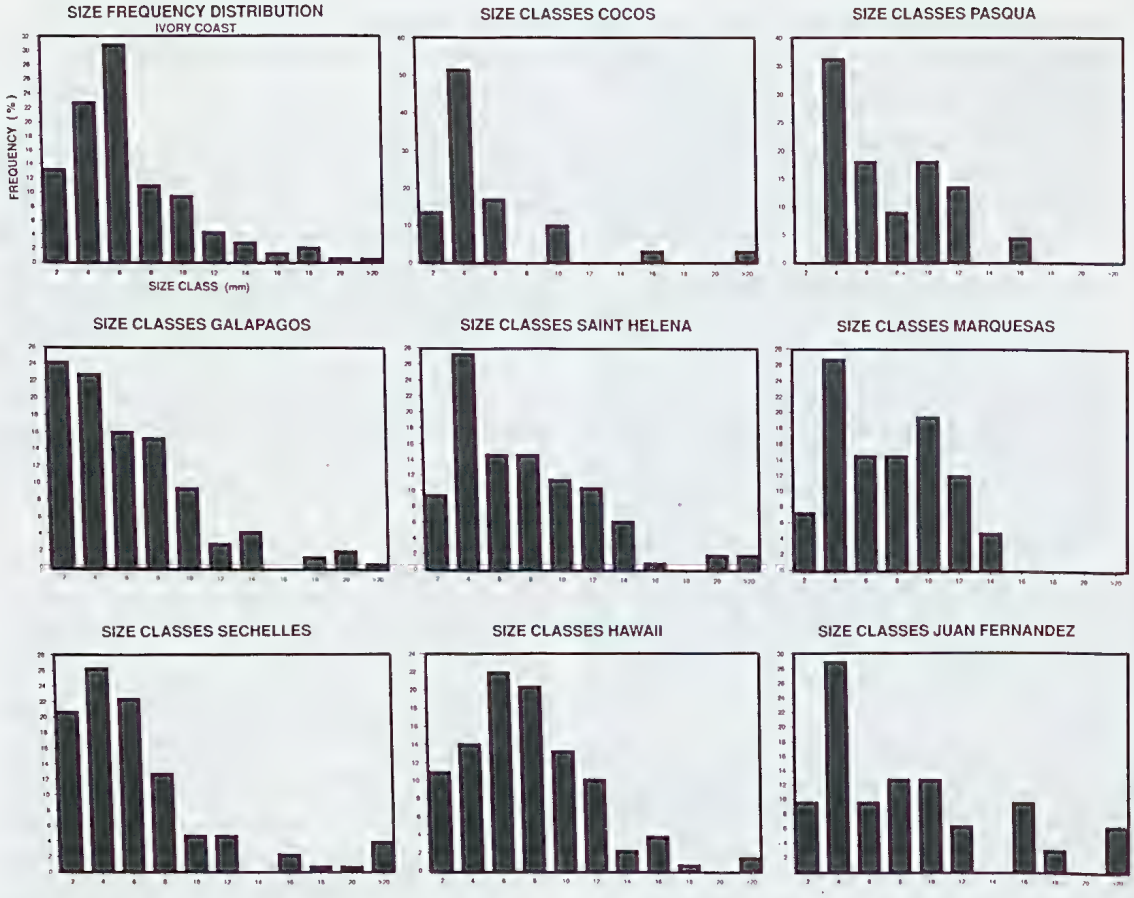


FIG. 2. Frequency distribution histograms of total body length (over 2mm size classes) for each island or archipelago.

equatorial archipelagos chain). In contrast, Hawaii and Galápagos have only a low percentage of Polynesian species as the distances between them and the Polynesian archipelagos are too extensive.

The term 'endemic' must be used now with great care because the continental faunas are far from being well known. This is especially so for the neotropical spider fauna. Many regions have been sampled only superficially or not at all. Few families have been thoroughly revised and new studies will be needed once the 'black holes' have been filled. For instance, the figures in table 2 for Galápagos are based upon 70% of the total of the recognised species. Hence, 46 species have yet to be identified. At this stage in our knowledge one is never sure that the species one describes from an oceanic island really has a dispersion restricted

Island/Archipelago	S	S/area	Continental distribution	Pacific origin	Cosmopolitan species	Endemic
Cocos I. (CO)	30	0.63	82% (A)			18%
Galápagos Arch. (GA)	146	0.02	32% (A)	4%	9%	60%
Hawaii Arch. (HA)	168	0.01	11% (A)	5%	19%	64%
Marquesas Arch. (MA)	48	0.04		31%	20%	50%
Juan Fernandez I. (JF)	32	0.18	17% (A)		17%	70%
Easter I. (PA)	23	0.14	22% (AU)		66%	12%
Seychelles Arch. (SE)	131	0.48	9% (E)		18%	65%
St Helena I. (SH)	98	0.81	7% (E)	44%	45%	

TABLE 3. The spider fauna of islands and archipelagos. Percentage of species with distribution 1° continental (A=American; E=African; Au=Australian), 2° cosmopolitan and 3° species known only from island or 'Endemic'. Values based only on described species.

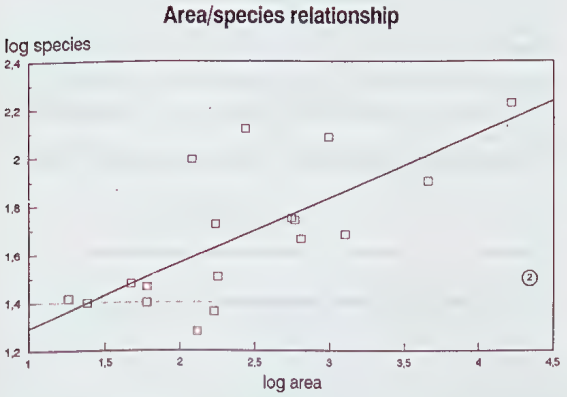
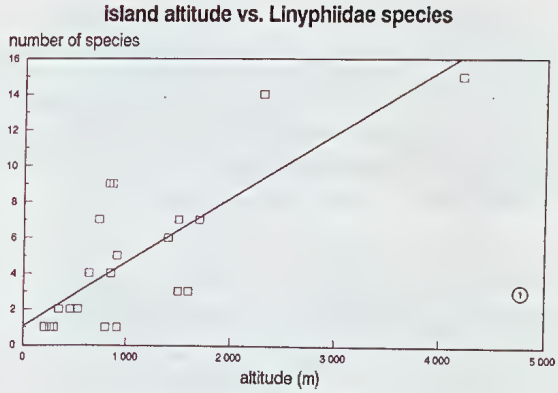


FIG. 3. 1, 2. Relationship between no. of spider species (N) and: 1, altitude (highest elevation) of island or archipelago (logN = -0.6224 log alt.(m)); 2., island/archipelago area (logN = 0.2686 log area + 1.0269).



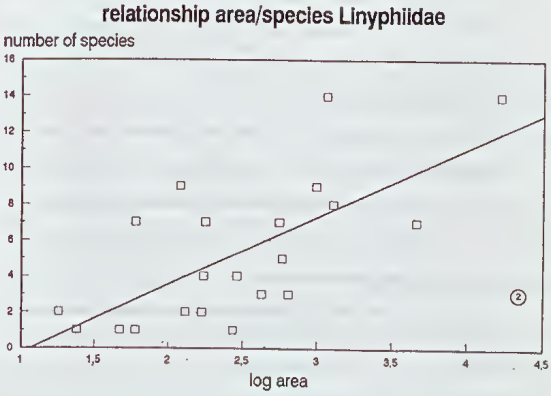


FIG. 4.1, 2. Relationship between no. of linyphiid species (L): 1, and altitude (L = 0.0035 alt(m) + 1.0544; 2., and island/archipelago area (L = 3.7886 log area - 4.0344) (separate islands in archipelagos). (S = no. species).

to that island for it may not yet have been found on the continent. We may therefore seriously question whether we can validly use the proportion of endemics for the analysis of an island fauna. However, we consider that the percentage of endemics we now recognise reflects the rough proportion of real endemics that will eventually be shown to exist.

Cocos Island seems to have few (18%) 'endemic' species. It lies relatively close to the continent. Once the distance to the continent exceeds 900km, we find an 'endemic' proportion in between 50 and 65%. The high percentage of 'endemics' on Hawaii (64%) is probably due to its old age and thus the long period of isolation of the archipelago. The high percentage for the Galápagos islands (60%) may perhaps be due to the fragmentary knowledge of the South American spider fauna (the main reason why one third of the Galápagos spider fauna is not yet identified).

The high percentage (70%) of 'endemics' on Juan Fernandez is very striking. Though close to the mainland, it is a rather isolated island (Humboldt Current) with an environment rendered harsh by the very special climatological conditions.

The proportion of cosmopolitan species on the islands varies between 0 and 20%, with two striking exceptions: Saint Helena with ca 44% and Easter Island with 60% (this figure is based on only 10 species). Most of these species are introduced and restricted to human settlements. This shows the great impact man has had on the spider fauna of Saint Helena.

All the islands considered here do have human settlements, native on Hawaii, Easter Island and Marquesas, but immigrated in historical times on the others. Human settlements invariably result in deforestation for arable land and subsequent introduction of ubiquitous species. Most often this is detrimental to the original fauna. Even more damage can be done with the introduction of

domesticated animals (cattle, dogs, cats, rodents, etc.) and cultivated plants. Accidental introductions can also have serious consequences as for instance the Little Fire Ant (*Wasmannia auropunctata*) on Galápagos. This species haunts large areas, devastating nearly all living animal organisms.

Qualitative Analysis

Qualitative analysis of the distribution of particular groups on islands is perhaps more revealing than quantitative analyses which are still hampered by the incompleteness of many data sets.

Spiders that do not balloon do not seem well adapted to colonise oceanic islands. Good examples are seen in the Zodariidae. Only four species, if we include *Cryptothele*, are present on the islands considered. On the Seychelles we find the endemic *Cryptothele alluaudi* Simon; the Comoros have *Asceua radiosa* Jocqué on Grande Comore and *Diores seiugatus* Jocqué on Mohéli (Jocqué, 1986). *Zodarion trispinosum* Suman is known from Hawaii. The presence of a *Zodarion* on Hawaii, completely outside its main distribution is puzzling, but is probably explained by an introduction as is the presence of *Z. fulvonigrum* (Simon) in North America. The Mygalomorphae are found only on two of these archipelagos. Six species in three families (Benoit, 1978) occur on the Seychelles. Five of these are endemic, the sixth species, *Idioctis intertidalis* (Legendre and Benoit), is also found on Madagascar and Grande Comore, where it occurs together with the endemic *Moggridgea nesiota* Griswold. The presence of these spiders, all but one apparently true endemics, on the Seychelles is explained by its granitic nature, which implies that they have had a fauna from the moment they were separated from the continent. The Comoros are probably more easily colonised than other islands, possibly by rafting, as that archipelago is close to its source area, Madagascar, for which the spider fauna is unfortunately poorly known.

Linyphiidae can be considered excellent colonisers mainly because many frequently balloon. However, linyphiids appear to be able to occupy few habitats. Jocqué (1984, 1985) explained that interference competition in tropical lowland with ants is apparently too important to allow the presence of many linyphiid species. As ants are less common at higher altitude many more linyphiid species tend to be present in highland than at low elevations (e.g. Scharff, 1992). (Since ant diversity and density are linked to climatic conditions, the impression may exist that they are the determining factor.) The presence of an important number of Linyphiidae on high islands was already illustrated for the Comoros (Jocqué, 1985). This is particularly true for islands. There is a significant correlation between the altitude of island and the number of species of Linyphiidae present (Fig. 4.1: $r = 0.780$, $p < 0.001$) and between area of the island and the number of linyphiid species present (Fig. 4.2: $r = 0.688$, $p < 0.001$). There is a third aspect relevant to the colonisation of islands: parapatric speciation on the spot. The Lycosidae are a good example. Wolf spiders might be expected to be good colonisers. Their juvenile stages are active ballooners, and transport by rafting is also a likely means of dispersal if only because lycosids are very common on banks of rivers and in marshes from where rafts are supposed to be derived. However, the number of insular species is quite low compared to the high number of species in continental tropical areas. (Galápagos: 6 species; Hawaii: 11; Cocos: 1; Juan Fernandez: 2; Saint Helena: 7; Seychelles: 2; Comorós: 3). Moreover, almost all species from islands in this study have no continental distribution and must be considered endemics of each island. Only *Bristowiella seychellensis* (Bristowe) is known from both Seychelles and Comorós. Their apparently high speciation rate may be related to this. Of special note, some species at high altitudes on some islands are apparently derived from species at low altitudes. A well documented case is that of *Bristowiella* on the Comoros where two closely related species have clearly differentiated habitats: *Bristowiella seychellensis* living in short grassy vegetation from sea level to about 1500m and *Bristowiella kartalensis* Alderweireldt living in recent lava flows with sparse vegetation from about 600m upwards (Alderweireldt, 1988). Another interesting case is that of the Hawaiian cave dwelling lycosids which have strongly reduced eyes or none and which clearly speciated on the islands themselves (Gertsch, 1973).

On Galápagos, a group of six species apparently derived from the most common one ('Lyc 3'). It occurs over the whole archipelago and occurs mainly in coastal salt marshes. Another species ('Lyc 5') occurs only on the low island Española. The four other species are confined to the high pampa zones of the volcanoes Sierra Negra and Cerro Azul ('Lyc 1') on Isabella, on San Cristóbal ('Lyc 2'), on Santa Cruz ('Lyc 4') and the Alcedo volcano on Isabella ('Lyc 6'). The revision of this remarkable species-group is in preparation.

A fourth example of such segregated parapatric populations is found on Juan Fernandez where 2 *Lycosa* species are found, one living along the coast, the other living in the higher pampa zone.

These statements reveal three important factors influencing the composition of island faunas. In the first place, there is the accessibility of the island, mainly its distance to a source area. In the second place, the diversity of the island's habitats is important. Particular spiders such as mygalomorphs and zodariids are only present on those islands that are easily reached or already had a fauna when they became isolated. Other families, although good colonisers, appear to be restricted by the ecological conditions of the island they can reach. Speciation appears to be the third factor which may be important in the colonisation of habitats that can hardly be reached by the normal ways of dispersal. The effect of niche pressure (Jocqué, 1982) is likely to be an important mechanism in this respect.

CONCLUSION

The faunal composition we now find on many islands is far from being natural. At the same time we know little about the arthropod fauna of most oceanic islands. This makes the analysis and comparison of the faunas very hard. The influence of speciation processes is probably largely overlooked in connection with the compensation of extinction.

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THE REPRODUCTIVE ECOLOGY OF *EUSCORPIUS FLAVICAUDIS* IN ENGLAND

T.G. BENTON

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The reproductive ecology of the scorpion *Euscorpius flavicaudis* was studied both in the field in England (at a colony dating back 120 yrs), and under semi-natural conditions in the laboratory. Before the mating season males become vagrant to search for females. On encountering a pregnant female or one with young, in her 'burrow', the male may mate-guard her until her period of maternal care ends and she becomes receptive to him. Large males have a higher mating success than small males. Two instars of adult males exist in this population of scorpions: large 7th instars and small 6th instars, and the reasons for this apparently paradoxical situation are explored. □*Euscorpius, mate-guarding, mating, life-history.*

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Evolutionary and behavioural ecology are relatively young disciplines; and have to date concentrated on using the more 'familiar' animals as subjects: birds, mammals and insects. These disciplines have largely passed arachnids by. Increasingly, however, we are beginning to realise the utility of arachnids as model animals in helping to elucidate general evolutionary principles.

Although there has been considerable increase in behavioural ecological interest in spiders in recent years, scorpions have been largely ignored. This is perhaps because they are difficult animals with which to work – long-lived, inactive, elusive and nocturnal. This paper outlines some of the main findings of a study of scorpion reproductive ecology. It is unfortunately incomplete: posing more questions than it solves; but, I hope that it illustrates the fact that, as in so many areas of their biology, scorpions are idiosyncratic, fascinating and more complex than they may first appear. This study combines the power of controlled laboratory experiments and the ease of laboratory observations with the reality of what is observed in the field; and, by so doing, for the first time the events surrounding the courtship of a scorpion are explored and placed in an ecological context.

THE STUDY ANIMAL

Euscorpius flavicaudis (de Geer), common throughout southern Europe (Birula, 1917), also occurs in England, most probably as a result of introductions. This species is a successful colonising species (Fage, 1928; Wanless, 1977; Lourenco & Vachon, 1981) and is often found associated with buildings (Wanless, 1977). Colonies have been reported from several locations in England, but only one, at Sheerness Docks, Kent (51°26'N, 0°45'E) has lasted many years and is of considerable size. The first record of scorpions at Sheerness is a label on a specimen of *Euscorpius flavicaudis* in the Natural History Museum, London: 'Taken in Sheerness Dockyard, 1870, J.J. Walker' (P.D. Hillyard, *in lit.*).

METHODS

Field Observations

At Sheerness Docks, most present buildings and the perimeter wall date from 1823 (Benton, 1992a). Scorpions are common in areas little frequented by people; and are especially common living in the perimeter wall. This old wall is about 4m high and 66cm thick. It shows the effects of time, with the mortar between the bricks crumbling away, creating 'cracks' which the scorpions readily inhabit. My study area was a 104m length of perimeter wall (bounding ornamental and vegetable gardens). The field study was conducted from January 1988 to July 1989, during which 92 visits were made to Sheerness Docks (totaling 500 hours of observations). Scorpions were observed using a portable ultra-violet light. Benton (1992a) details field methods.

Laboratory Observations

To allow more complete observations and experimentation a laboratory colony of *Euscorpius* was set up, modelled on the habitat at Sheerness. This consisted of a plywood wall (2.44m x 5.79m), covered in sandpaper, with 144 slots (2.5

x 5.1cm) cut into the face. Into these slots were fitted artificial 'cracks' 12 cm long. These were open to the wall and closed at the far end. A layer of soil was placed at the base of the wall. This soil was periodically damped to mimic rain; and each week woodlice (the scorpion's natural food) were released onto it. This colony was kept under a natural photoperiod, and as near natural temperature and humidity as possible. Observations and experiments were conducted at night, when the wall was illuminated by lamps fitted with deep-red filters (invisible to scorpions: Machan, 1968). Unless being used in an experiment, the scorpions (collected at Sheerness) were allowed to move freely around the wall. Benton (1991a) details colony setup.

Experimental Methods

In this study of male contest behaviour for females during the mating season, 11 males were used. On the artificial wall 40 x 40cm enclosures were made around a single crack. A female carrying young was placed in this crack, and later an experimental male was added. Thirty minutes after this male had encountered and entered the crack a second male was added. After encountering the crack the second male would attempt to enter. The males would then meet, assess each other and fight. This procedure was then immediately repeated. The two replicates constituted a 'contest' (and in all cases the results were unambiguous, and identical for each replicate). In total 110 contests were conducted (with each male as 'owner' against every other male as intruder). Contest order was randomly selected. Other methods are detailed in Benton (1992b), and scorpion mensuration in Benton (1991b).

RESULTS

Background

Like most scorpions, *E. flavicaudis* is nocturnal. During the day and over the winter, they are not visible as they have retreated to the back of their cracks in the wall. At night, depending on the season, most scorpions evident are at the entrance to their cracks where they remain immobile, with their claws outstretched and open. The most common prey items are isopods (*Porcellio scaber*) (64%) and then conspecifics (12%) (Benton, 1992a).

Seasons

Scorpion activity at Sheerness is highly seasonal. Over the winter very few (if any) can be seen. The numbers build up during the spring and peak in late summer (Benton, 1992a) before decreasing again to winter levels. As these scorpions live for several years (Benton, 1991b) this pattern reflects varying patterns of behaviour, rather than gross mortality and natality. For most of the year, most scorpions seen are in their crack (for November to June only $8 \pm 11\%$ of all scorpions observed are out of their cracks). However, in summer, on average, $24 \pm 9\%$ of scorpions observed were on the wall surface. Adult males make up most surface-active animals: 3-4x more males are seen on the wall surface than adult females over the summer (Figs 1a, b).

The number of females giving birth or with young peaks when female activity on the wall surface (Fig. 1a) is least. Females with young remain deep within their cracks, and were never observed to venture onto the wall surface. Indeed, females in the last stages of pregnancy also appeared to show a marked reduction in activity.

Most matings at Sheerness (Fig. 1b) are just after the number of females with young peaks (Fig. 1a). Known females with young were found to be unreceptive to males until 2 ± 1.2 days (n=12) after the juveniles had moulted and climbed off her dorsum (Benton, 1992b).

About 3 weeks after male surface-activity begins, the number of matings observed peaks (Fig. 1b). Only at this time can males and females be found together in the same crack. These periods of cohabitation averaged 10 ± 9.9 nights (range 1-30; n=19; data from field). Cohabiting occurred only prior to mating, and whilst the female was either carrying young, or in late pregnancy (Benton, 1992b). Males were associated sometimes with females living in shallow cracks (n=3); in which case the males spent the day in a deep crack nearby and 'commuted' to the female's crack to spend the night sitting at the entrance. The identity of the male mating with a specific female was known for 15 cases of cohabitation: in 14 the male had been recently cohabiting ($P<0.005$) with that female. Females of this species do not appear to assess males, and will mate with any male present when they become receptive (Benton, 1992b). If a male's encounter rate with females is low, and a female's receptivity is predictable, then a male encountering a soon-to-be receptive female may do better waiting for her to become receptive, rather than leaving her and risking trying to find a female nearer receptivity (Grafen and Ridley, 1983); and this seems to be the case with these scorpions (Benton, 1992b). This behaviour can also benefit

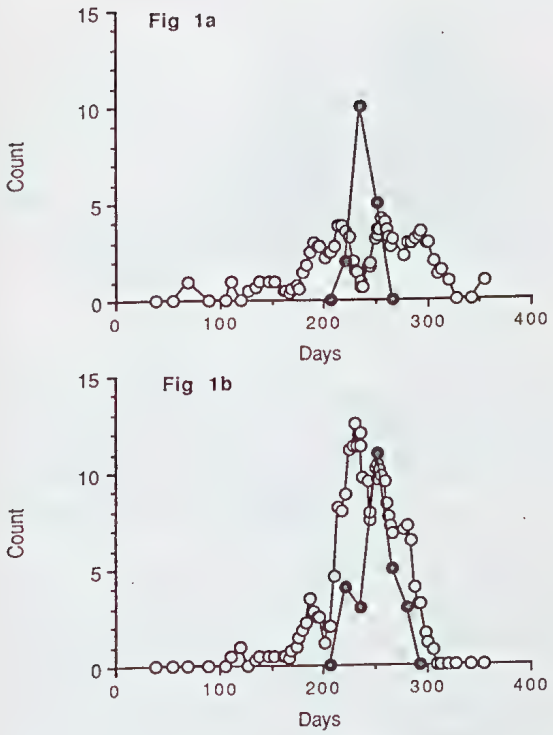

FIG. 1. Reproductive season of *Euscorpius flavicaudis* in England, 1988. (a) Seasonality of adult female surface-activity and no. of births. Female surface-activity is smoothed over two weeks: nightly count shown as average of preceeding and following week's counts. No. of births (for each half-month) estimated from no. of females giving maternal care, and date at which this ended. (b) Seasonality of adult male surface-activity (smoothed over two-weeks), and half-monthly count of no. of matings (observed no. of matings plus no. of spermatophores found). Data originally, in part, in Benton 1992b.

the females for two reasons. Firstly, it ensures that they are mated. Secondly, a major advantage of maternal care in scorpions is to prevent predation of the juveniles (Benton, 1991a), so having a male at the front of the crack prevents entrance by other scorpions which may aid this role.

In all cases of cohabitation, the male stations himself near the entrance, with the female behind him. Males attempting to enter the crack encounter the currently cohabiting males, and each tries to grasp the other's claws. Within a very few seconds one male retreats and flees from the crack. Males therefore fight for 'possession' of a crack occupied by a female in the period before she becomes receptive.

To investigate male mate-guarding contests 110 contests were staged between 11 males (each male as 'owner' against each of the others as 'intruder'). The proportion of contests won correlated very strongly with measures of scorpions size, and most strongly with pedipalpal claw length (r_s=0.97, P<0.001). This is to be expected as *E. flavicaudis* uses its claws as its main offensive weapon. In 80% of contests, the larger-clawed male won; when the smaller-clawed male won (20%), it was the 'owner' in most (91%) contests. Both relative claw-size and ownership status had highly significant effects on contest outcome (two-way ANOVA, size: F=68.5; df 1,36; P<0.0001; status: F=42.7; df 1,36; P<0.0001): large-clawed males usually won contests, but if contestants were closely matched in size then ownership status decided the outcome (giving an advantage equivalent to about 11% longer claws).

Size and Sexual Advantage

In the laboratory, males differed in reproductive success: some males mated twice, some once and some not at all. Larger males mated more often than small males (Fig. 2). This size advantage is for two reasons. Firstly, as described above, larger males are better competitors for female-occupied cracks. Secondly, about 40% of matings are not preceded by mate-guarding. These fall into three broad categories: non-pregnant females at the start of summer, females not found by males before their maternal care has ended and (most rarely) females who have mated already (this is possible as a spermatocleutrum is not secreted in this species). Large males obtain more matings from all three categories than small males. This is because, for each category of mating, females are initially unwilling to court. When a female is mate-guarded prior to her receptivity, she encounters the male frequently, and upon becoming receptive begins courting without aggression. Conversely, when a male encounters a non-pregnant female, or one without young he immediately attempts to court. The male grabs (or attempts to grab) the female's claws and stings her (Benton, 1990). Indeed, the start of a courtship (without mate-guarding) is indistinguishable from a cannibalistic attack. Large males are better at mating with these unwilling females as, unusually for scorpions, large males can be larger than females. In this species, and others (Polis, 1980), size (especially claw-size) is a good predictor of the outcome of cannibalistic contests. At the start of courtship, males

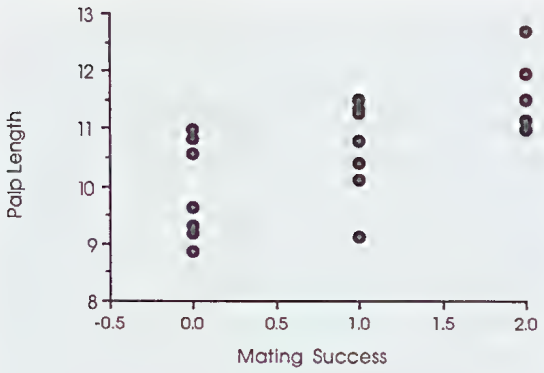

FIG. 2. Relationship between size (claw-length) and mating success in laboratory males free on wall surface (mean ± SD). Difference between groups is significant (Kruskal-Wallis, H=11.4, P=0.003).

sting females, and larger males can eat adult females (and often do: 10 cases observed in the laboratory), therefore, large males essentially give females the choice of being cannibalised or accepting courtship. Small males obtain fewer matings as they have a smaller (or nonexistant) size-advantage over females (Fig. 3) and therefore are more likely to flee from those females who are not immediately willing to court.

Size Dimorphism

Sexually mature adult males are recognised by the secondary sexual characteristic of a notch in the pedipalpal fingers (Fig. 3). Adult males can differ markedly in size, and this is especially noticeable when one considers claw size, which increases allometrically with body size, such that larger males have disproportionately larger claws (Fig. 3). The frequency distribution of adult male claw sizes at Sheerness was dimorphic (Fig. 4). This dimorphism also occurs with other measures of size, such as prosoma length (Benton, 1991b). This dimorphism probaly arises because there are two instars of adult male in the population at Sheerness: 6th and 7th (see also Benton, 1991b).

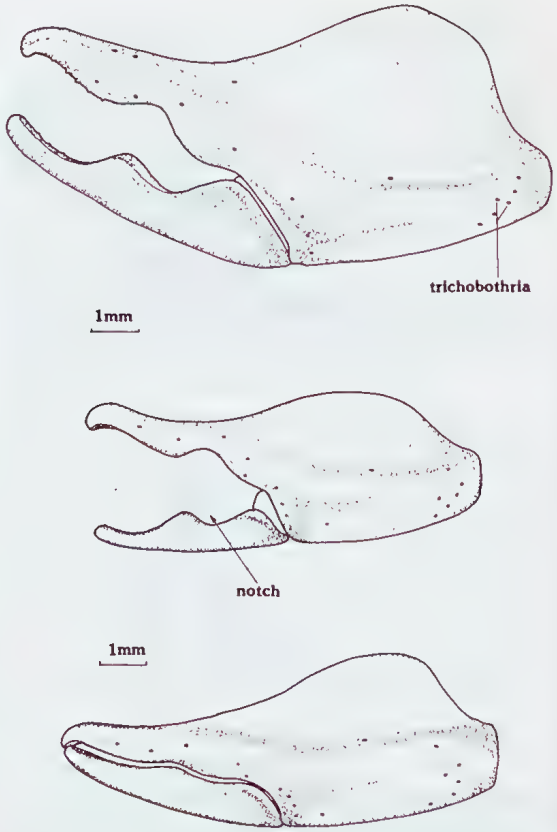

FIG. 3. Claws of two adult ♂ ♂ (a, b) and one adult ♀ (c) same scale. Note secondary sexual characteristic: notch in fingers.

DISCUSSION

Two points are noteworthy. Firstly, the reproductive ecology of *Euscorpius flavicaudis* is much more complex than previously imagined. Naively placing pairs of scorpions together in a laboratory situation to watch the courtship would present a very misleading picture because the most significant behaviours occur before actual courtship. Precopulatory mate-guarding has not been reported in scorpions, but is known to occur in some spiders (e.g. Vollrath, 1980; Watson, 1990) and occurs widely across the animal kingdom (Ridley, 1983). For precopulatory mate-guarding to evolve, males must gain an advantage by staying with a female prior to her becoming receptive rather than searching for a receptive female. Two criteria may determine this situation: firstly, if a male can predict when a female is going to become receptive, and, secondly if receptive females are difficult to find. The former may occur if females become receptive following a moult (e.g. Watson, 1990), or as in the case of these scorpions, after maternal care. The latter criterion may result from female receptivity being very limited in time (e.g., in *Gammarus* female receptivity is limited to a brief period between moulting and the hardening of the amphipod's exoskeleton: Grafen and Ridley, 1983), low population densities (and so low encounter rates) or because of high male mortality

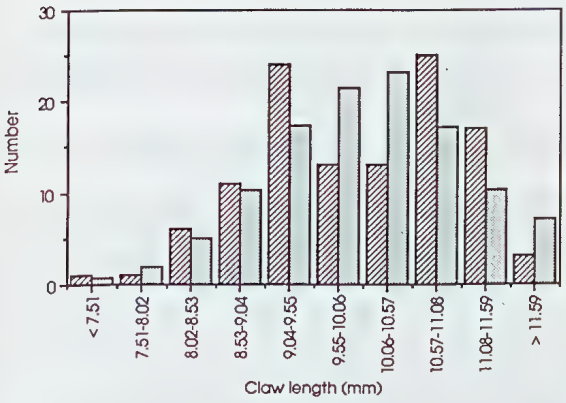

FIG. 4. Distribution of claw-sizes in adult ♂♂ is significantly non-normal. Filled bars are observed distribution; stippled bars are expected normal distribution given mean and standard deviation of data. (χ^2=21.1, P<0.005).

during mate-searching (Vollrath, 1980). The period of female receptivity is reduced where the paternity of a male is ensured by being the first male to mate with a female (so called first-male sperm priority), which may be common in arachnids (e.g. Vollrath, 1980; Watson, 1990). A virgin female is far more valuable to a male than one which is already mated. Thus, *Euscorpius flavicaudis*, first-male sperm-priority and low population densities, coupled with the female's receptivity being predictable, may make it more profitable for a male encountering a female engaged in maternal care to mate-guard her rather than risk searching for another female nearer receptivity.

Secondly, there seems to be a paradox. Adult males exist as two instars in the population. This itself is not a novel finding (see Francke and Jones, 1982). It is surprising that any males mature at the smaller instar since the smaller males seem to be at such a disadvantage in obtaining mates. Natural selection would quickly eliminate any tendency to mature at a disadvantageous size.

The paradox suggests two explanations. First, large males may have an advantage only in a mating season. As large males have more instars, they probably take longer to mature. Although males mate more in the short-term, the younger they mature presumably the more seasons in which to find mates. Perhaps there is a mixed evolutionarily stable strategy (ESS) such that the short-term gains enjoyed by 'large males' are offset by the losses due to having one less season in which to mate, so that, on average, the lifetime reproductive success of 'large' and 'small' males is equal. This ESS could be maintained by frequency dependent selection (Benton, 1992b): large males do relatively better when rare (as they suffer little competition) so their frequency is increased in the population by natural selection. However, when large males are common their gains are reduced, because of increased competition between them, to a point where they are offset by the cost of delaying maturity. Hence, an evolutionary equilibrium is reached between the genes controlling maturation at the 6th and 7th instars.

Secondly, an alternative explanation for this paradox is that there may be phenotypic plasticity in the maturation stage. A gene that can produce a variety of phenotypes depending on the environment is said to exhibit phenotypic plasticity (Lessels, 1991). The 'optimal' time at which to mature may depend on factors such as food availability, and thus growth rate (Stearns and Koella, 1986). For example, if food is plentiful, and an individual is large for its cohort it may be best to mature early. Conversely, if an individual is small for its cohort then it may be better to delay maturity until more food is encountered. This seems to be the case in many spiders (e.g., Deevey, 1947; Vollrath, 1980). This subject will be discussed further elsewhere (Benton, in preparation).

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COMPARATIVE POSTEMBRYONIC DEVELOPMENT OF ARACHNIDS

ALAIN CANARD AND ROLAND STOCKMANN

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A common model is used to describe the growth of various arachnid groups. In these predators there is retardation of development of the first instars, along with greater maternal care for the clutch and even, as far as some groups are concerned, in a viviparous development. Mites, which have very diversified biologies, have developments which have evolved in many different ways.

Les développements des différents groupes d'arachnides sont décrits en suivant une trame commune. Il apparaît ainsi une évolution des groupes de prédateurs qui se traduit par une augmentation du retard de développement des premiers stades, en liaison avec des soins à la ponte croissants, avec même pour certains groupes des développements vivipares. Les Acariens, de biologies très diverses, ont en conséquence des développements qui ont évolué dans des voies très différentes.□*Development, arachnids, growth.*

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19 March, 1993.

Analysis of developmental types used in arachnids is very great diverse in the terms used to describe these phenomena. This diversity tends to partially hide some similar points in the developmental process. Authors often use terminology and analyse specific to a single group or species, instead of referring to general concepts relating to all arthropods.

This study compares the developmental processes using the same terms, and we will only use specialised terms if it is absolutely necessary. All developments cannot be discussed in detail here; definitions and more precise descriptions can be found in Canard and Stockmann (1992).

METHODS

Our study is based mainly on literature, enriched with our observations on arachnid growth, particularly on spiders and scorpions.

First, we will evoke the main concepts and definitions used and will then define the different scales of development for each taxon. Taxa which are exclusively predatory are here represented by to the increasing level of care devoted to the clutch. Mites, which have diverse biologies, will be studied separately later.

RESULTS

Concepts and Definitions

POSTEMBRYONIC DEVELOPMENT, HATCHING AND BIRTH

The development, defined as initially embryonic, starts with the first divisions of the egg and continues with the formation of tissues. After hatching or birth, the development is qualified as postembryonic. The postembryonic organism is then covered with an external integument and develops outside of the egg membrane or the female's genital tract. Various organs appear and develop, some will not be functional until late developmental stages (e.g. genital organs). Externally, the development is shown by changes in the cuticle. Reiteration of this concept may seem pointless, but the study of arachnids requires some explanations about hatching and birth.

Hatching, i.e. the opening and release from the egg's membrane, can be a long process. It may take a few days for some spiders, and sometimes some moults can be observed between the beginning of the opening of the egg's membranes and their complete liberation. Hence, the postembryonic period does start with the opening of the egg's membranes. This does not make it necessary to look for a phenomenon before hatching as, for example, Legendre (1958) and Vachon (1958b) did as they chose the 'inversion' to define the beginning of the postembryonic period. Moreover, this proposition has one drawback: it makes the postembryonic development begin at a time when the organism is not covered by a tegument.

Birth appears as a well and easily defined phenomenon, without ambiguity. However, in pseudoscorpions, the organism leaves the female's genital tract and moves into a ventral

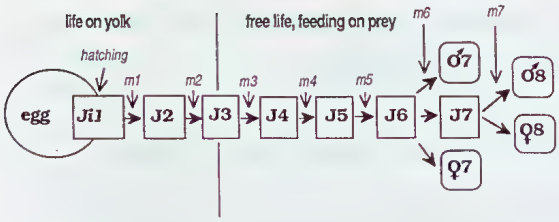

FIG. 1. Stages of postembryonic development of an opilionid, *Liobunum rotundum* (Phalangidae, Palpatores) (after Gueutal, 1943 and Naisse, 1959). (m = moult, **Ji** = incompleted juvenile, **J** = juvenile).

brood pouch, which is like an external extension of the female's genital tract. Once in the pouch, development continues and the organism still receives nutritive fluid from the mother. Therefore, the start of the postembryonic development of pseudoscorpions should be when they leave the pouch, rather than when they leave the female's genital tract, as others have stated.

INSTARS AND STASES

The instar is the organism between two moults. Generally, among arthropods, the external form does not significantly change between these two stages, except for the short periods of pre- and post-exuviation. However, among some mites, the external morphology and biology are modified while the cuticle remains. Hence, Henking (1882) distinguished two forms, called instars ('stade'), one active and the other motionless. Although this use of the term 'instar' was followed only by a few authors to describe the development of few mites, another acarologist (Grandjean, 1938), considered that the term was too indefinite and proposed the term 'stase'. The definition of stase changed later, but this term is the basis for an evolutionary concept (Grandjean, 1954; André and Jocqué, 1986; André, 1989).

We use 'instar' here in its usual definition, which means an organism between two moults (for endocrinal considerations, see Canard and Stockmann, 1992). To keep the general definition, we will discuss the concept of stase later. When the animal presents separate biologies linked with two different aspects during the same instar, we call them 'forms' and give them two different names.

SUCCESSION OF INSTARS

We limit our study to a morpho-biological description of the successive instars. These instars can follow each other in phase (Vachon, 1953) in which all instars are of same kind. These different types are defined in Table 1.

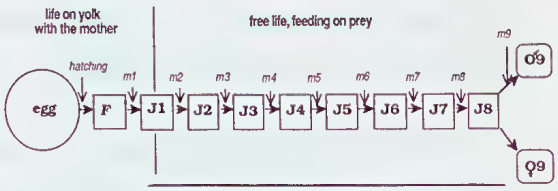

FIG. 2. Postembryonic development scheme of a solpugid, *Eremobates durangonus* (after Muma, 1966).

DIFFERENT DEVELOPMENTAL ROUTES

OPILIONIDS

The eggs are laid isolated from each other and then abandoned. The emergent animal depends on its yolk reserves. It looks like a juvenile harvestman but morphologically differs from following instars by the unpigmented integument and lack of some characteristics, such as unformed chelicerae, unsegmented tarsus, absence of median eyes, etc. Therefore it is an incomplete juvenile: $\mathbf{Ji_1}$ (term taken from Holm, 1940 concerning spiders) (= 'larve' according to Juberthie, 1965). It also has temporary organs (one or two egg teeth located on dorsum of cephalothorax).

After the first moult, the animal differs from the imago only by its size and by sexual characteristics. It is a juvenile, the second of the juvenile phase: $\mathbf{J_2}$ (= 'nymphe' according to Juberthie, 1965). Although active, it still lives on its yolk reserves. After one moult, the juvenile opilionids ($\mathbf{J_3}$) scatter and then feed on prey they catch. Usually, 6-7 juvenile instars occur before it becomes an imago, more rarely there are 5 to 8. The number of moults may vary from with individuals of a species, and according to the developmental conditions; this number is generally the same for both sexes.

On becoming a breeding instar (imagos) the opilionid cease moulting (adults), although some may live for be 5-6 years (Juberthie, 1965).

SOLIFUGIDS

The female isolates herself in burrow but does give care to her eggs.

The animal which hatches is incomplete, motionless and lives on its yolk reserves. It is unpigmented, has no eyes and no racquet organs. Two types may be distinguished. The first is in the Galeodidae (Vachon, 1958a; Junqua, 1966). It does not look like the imago and keeps the aspect it had while under the constraint of the membranes of the egg; it is a foetal instar: **F** (= 'larve' of Vachon, 1958a or Junqua, 1966, = 'post-embryo' of Muma, 1966). The second type is present in some Solpugidae (Lawrence, 1947)

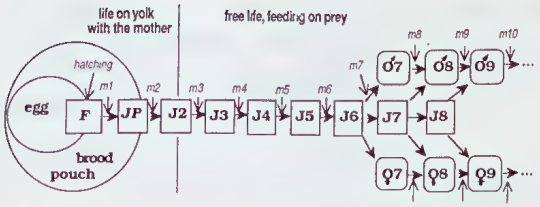

FIG. 3. Scheme of the different stages of the postembryonic development of an amblypygid, *Tarantula marginemaculata* (after Weygoldt, 1970).

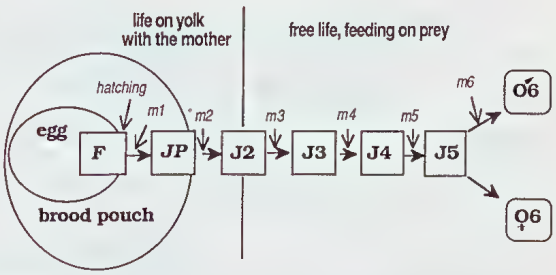

FIG. 4. Scheme of the different stages of the postembryonic development of *Typopeltis stimpsonii* (Thelyphonidae) (after Yoshikura, 1965).

and some Karschiidae (Thaler, 1982). It looks like the imagos (juvenile), but lacks some structures and has temporary organs like thorny continuations of the legs. It is an incomplete juvenile: Ji_1 (= 'primärlarve' of Thaler, 1982).

A further moult results in an animal which has all the adult organs, except those linked with reproduction. This juvenile is, according to the species, the first or the second of the phase (= 'nymphe' of Vachon, 1958a; Junqua, 1966; Muma, 1966). It remains with the female until its integument is hard enough, then it disperses and lives on its own, feeding itself on prey it catches. The number of instars before reaching the status of imago varies according to the individuals. The imagos have a short life expectancy comprising only one instar (adult).

Amblypygids

The female carries the eggs under its abdomen in a brood pouch generated by the genital tract during egg-laying. The incubation period of the clutch may last 3 months (Weygoldt, 1970). Hatching takes place in the brood pouch.

The organism released from the egg's membranes has a foetal aspect with the prosoma bent towards the abdomen and its appendages tight along the body. It is very incomplete (appendages incompletely segmented, absence of setae and of sensory organs, etc.), motionless and lives on its yolk. It is a foetal instar: **F** (= 'deutembryo' of Weygoldt 1970).

After one moult, the animals leave the brood pouch and attach themselves under the females's abdomen. They still live on their yolk, can move, and look like imagos (juvenile), but some structures are lacking and the internal organisation is incomplete (digestive tract, circulatory system, etc.). It is an incomplete juvenile instar which has particular organs on the legs, a dorsal continuation at the distal end of the tibiae (Weygoldt, 1970) and, in some families, an adhesive organ at the tip of the tarsus. It lives on the mother and is adapted to this life, so with reference to Scorpions, we call it the pullus: **JP** (= 'embryon' of Pereyaslawzewa 1901, and 'praenymphe' of Weygoldt 1970).

The pullus moult while on the mother and then leaves her. Through this moult it acquires all the characteristics of the adult (except the reproductive organs). It is a juvenile instar: J_2. After a short gregarious period, the juveniles scatter and live on their own, feeding themselves. The number of juvenile instars may vary between individuals (Weygoldt, 1970) and, after one year, they become an imago.

The imagos of both sexes go on moulting and, under good conditions, the females keep growing after this moult. Therefore, there are no 'adults'.

Uropygids

The female isolates herself in a burrow, and lays her eggs in a newly secreted transparent ventral sac.

Hatching occurs in the brood pouch. It corresponds to a quasi-simultaneous release of the egg's membranes and of the integument of an instar similar to the foetal instar of the Amblypygids: **F** (= 'primärlarve' of Kästner, 1949 and 'prelarva' of Yoshikura, 1965). This instar, which was already formed in the egg, has a very short postembryonic life.

The animal released after hatching and after the first moult, can move and climb upon the mother's back. In general morphology, it looks like the adult (juvenile phase), but lacks some organs (median and lateral eyes are not yet visible, flagellum unsegmented, etc.). It has particular organs linked with its life on the mother, including pad-like organs at the tip of the legs, instead of claws. It is a pullus: **JP** (= 'sekondärlarve' of Kästner, 1949; 'larva' of Yoshikura, 1965). After a 'diapause', there is a moult which releases a juvenile instar: J_2 (=

Forms	Characteristics			Symbols
Non-breeding	different morphology from imagos	motionless instars which do not feed themselves	embryonal aspect unsegmented appendages	foetal instar
			segmented appendages	nymph
		active instar		larva
	same morphology as imagos	several organs which do not function	no temporary organs	incomplete juvenile
			temporary organs linked to life on mother	pullus
		only non-functional genital organs		juvenile
Breeding (= imagos)		with moulting		imago

TABLE 1. Characteristics of different kinds of instars.

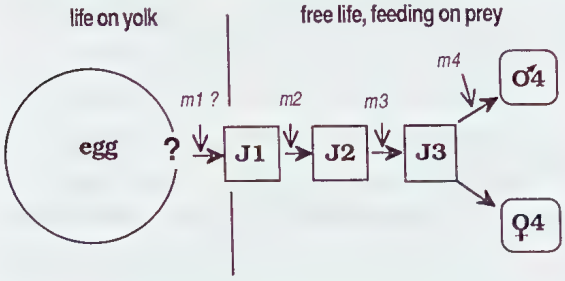

FIG. 5. Scheme of postembryonic development of *Prokoenenia wheeleri* (after Rucker, 1903).

'pullus' of Kästner, 1949; = 'protonymph' of Yoshikura, 1965). They are still gregarious but move around the burrow and begin to feed themselves. After one winter spent together, they then moult and scatter. Subsequent moults usually occur annually, but may be less frequent (Yoshikura, 1965).

Imagos do not seem to moult (adults). Their size of each species does not vary much.

Palpigradids

The sexual biology of palpigradids is almost unknown. Moreover, nobody has ever succeeded in breeding palpigradids. Therefore, knowledge about their postembryonic development is based on observations of natural populations. Under these conditions three immature instars have been determined for many species (Condé, 1984).

The three instars of *Prokoenenia wheeleri* correspond to juvenile instars (Rucker, 1903). Their morphology evolves in a quantitative manner (number of bristles, articulations of the flagellum, evolution of genital parts, etc.).

Spiders

The degree of maternal care given to the clutch varies between species. Some spiders abandon their cocoon (e.g. araneids). Others carry it in their chelicerae or attached to their spinnerets.

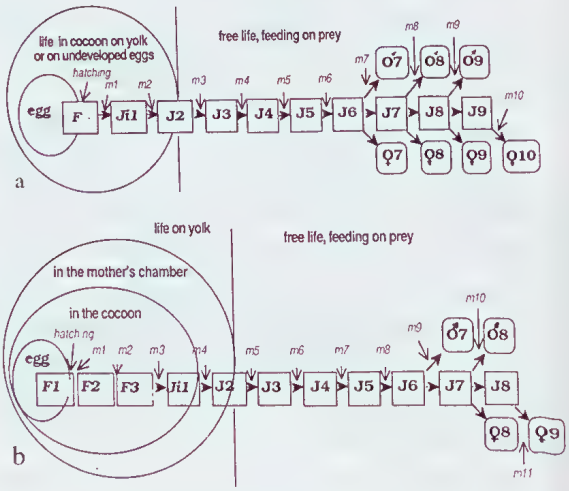

FIG. 6. Postembryonic development in two spider species that (a) abandons its clutch (*Larinioides cornutus*) (after Ysnel, 1992), and (b) cares for young (*Philaeus chrysops*) (after Bonnet, 1933; Canard, 1984).

Others keep their clutch with them in their silk chamber (e.g. salticids).

Hatching occurs in the cocoon and it sometimes takes a few hours before the first instar is released. This instar is generally foetal: **F** (= 'prélarve' of Vachon, 1958b, = 'pullus' of Canard, 1984). Among some orthognathids it remains intrachorional and is therefore not postembryonic. Its very thin cuticle bursts during hatching when the egg membranes open. Among several species which give care to the clutch, there is a series of 2 or 3 instars of this kind: $\mathbf{F}_1$, $\mathbf{F}_2$, $\mathbf{F}_3$ (Canard, 1987). As they cannot move, they stay in the cocoon.

The following instars are mobile and look like a spider (juvenile) but the first one or two still lack some adult characteristics: they are incomplete juvenile (**Ji**) (= 'larves' and 'prénymphes' of Vachon, 1958b). In some cases, the first instar of

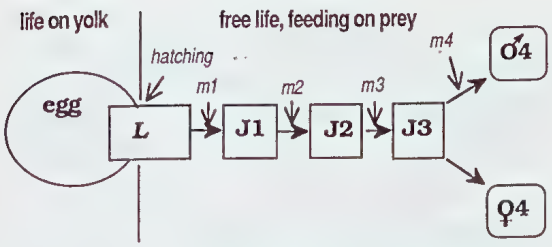

FIG. 7. Scheme of postembryonic development stages of ricinuleid *Crytocellus palaezi* (after Pittard and Mitchell, 1972).

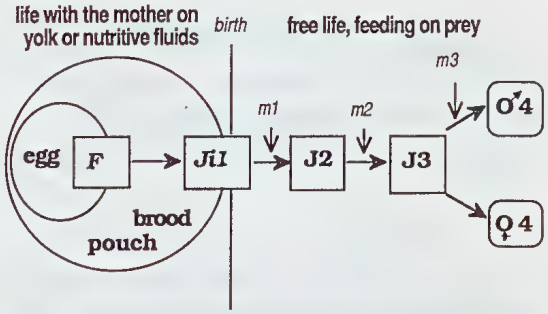

FIG. 8. Postembryonic development of a pseudoscorpion, *Chelifer cancroides* (after Vachon, 1938).

this phase is very incomplete, but in some others, some characters can only be shown absent using an SEM. These first incomplete juvenile instars live on their yolk, but some also feed on undeveloped eggs, which they can pierce with a cheliceral blade. Dispersal takes place after the moult which releases a juvenile equipped with all its organs (**J**). Juveniles then live on prey they catch (= 'nymphes'; Vachon, 1958b). The total number of juvenile instars may vary within a species. Males often become an imago in fewer instars than females.

Female orthognathids and filistatids can still moult. In labidognathids, imagos do not moult any more (adults). In nature, all male spiders die without moulting.

Ricinuleids

Hatching releases an active individual, which catches prey but which has only three pairs of legs and therefore does not present the general arachnid characteristics. It differs from the imago, and is a larva: **L**. The three instars that follow resemble the imago, and possess 4 pairs of legs; however, they lack genitalic structures. They are juveniles instars: J_1, J_2, J_3 (= 'nymphes' of Pittard and Mitchell, 1972). There is only one imaginal instar (adult).

Pseudoscorpions

The eggs are laid in a brood pouch where they feed upon maternal nutrients with the aid of the embryonic membrane. Growth of the embryos bursts the chorion and the external side of the brood pouch to which they remain attached by the buccal region. Their form is not differentiated. Within a few seconds, the mother injects a nutritive fluid which trebles their volume (= 'larves gonflées' of Vachon, 1938; 'deutembryons' of Weygoldt, 1969). Organogenesis continues and a moult occurs which releases an animal which emerges by an anterior cephalothoracic tooth.

The released instar looks like the imago, but retains some non-evolved characteristics (sensorial system, silk glands, digestive tract, etc.). It is an incomplete juvenile: Ji_1 (= 'larve II' and 'protonymphe' of Vachon, 1938; 'protonymph' of Weygoldt, 1969). Some species apparently retain a foetal aspect (Judson, 1990). The first free instar sometimes remains and moults in the chamber constructed by the female (Weygoldt, 1969). The animal lives alone after this moult. The number of following juvenile instars is fixed to two: J_2 (= 'deutonymphe'), J_3 (= 'tritonymphe'). Each instar can be identified through its trichobothriotaxy (Vachon, 1938). Imagos do not moult any more.

Scorpions

Eggs hatch in the female's genital tract (viviparous species) or soonafter laying (ovoviviparous species).

Newly born scorpions climb onto the mother's back and remain there, living on yolk reserves. They resemble an adult (juvenile) but is incomplete (without trichobothria, unpigmented integument, without specific bristles, etc.). It has temporary organs linked to life on the mother's back, such as legs without claws but bearing adhesive organs at their tip. This incomplete juvenile is a pullus: **JP** (= 'larve' of Vachon, 1940).

After one moult on the mother's back, the juveniles periodically move to the ground, where they begin hunting and eating for the first time. They disperse afterwards and live alone. The second instar is a complete one (J_2). The number of juvenile instars may vary according to sex. Mostly there are 6 to 7 instars, but it may vary from 5 (*Orthochirus*) to 10 (*Diplocentrus*) (Polis, 1990). Imagos do not seem to moult, but it may be possible (Stockmann, 1968).

Mites

The Acari have many more developmental

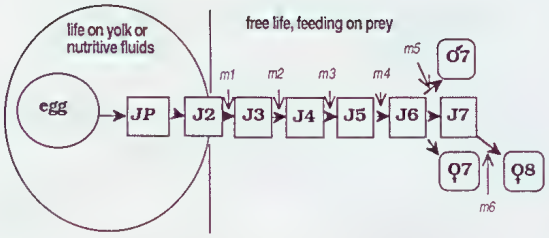

FIG. 9. Postembryonic development stages of a scorpion, *Euscorpius italicus* (after Angermann, 1957).

types than other arachnids. The eggs are often abandoned. There is a first instar which has a foetal aspect, but it remains intrachorionic, except in some cases (Coineau, 1977). This instar can be compared with foetal instars of other arachnids (**F**), but it is not postembryonic.

The first free instar is obviously different from the imago because it usually has only 3 pairs of legs. It moves and can feed itself. It is a larva: **L**.

The following instars are eight-legged and only differ from the imagos by some quantitative or sexual characteristics: they are juveniles (**J**) (= 'nymphes'). The number of instars is often fixed for a species, at 1 or 2, more often a maximum of 3, but up to 4-5 in the Argasidae.

After these immature instars imagos appear, which do not moult anymore (adults) (= 'prosopon' of Reuter, 1909).

In the thrombidiids, there are periods of inactivity between larval and juvenile stages and between juvenile and adult stages. At such times, the animal is covered by the original cuticle, but secretes a new tegument under it, which becomes the tegument of the next instar. In many other cases, motionless instars can be distinguished, sometimes comparable to real nymphs or to specific survival-forms, which allow for dispersal.

DISCUSSION AND CONCLUSIONS

Terminology and Concepts

Most terms used in other arthropods can also be used in arachnids. We have used only the original terms of pullus, foetal instars and incomplete juvenile.

The foetal instar, although it has been defined for arachnids (Canard, 1987), is not specific to this group. It is evident in some insects and myriapods (= 'prolarves', 'prélarves', 'pseudo-foetus', etc.).

The incomplete juvenile instars belong to the juvenile phase of which they form a part (J_{i1} followed by J_2). One can recognize the sys-

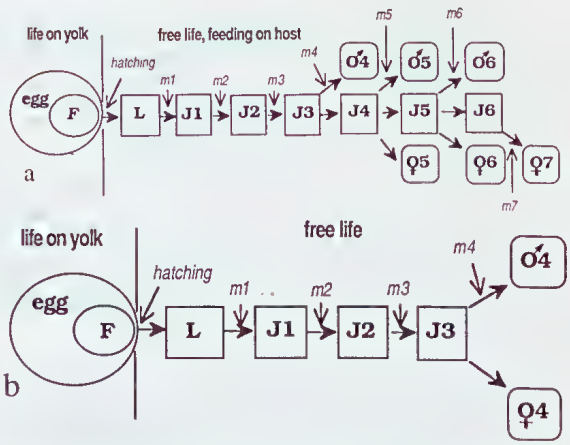

FIG. 10. Succession of stages in postembrional development of mites, (a) Argasidae, *Ornithodoros maritimus* (after Guiguen, 1990); (b) Oribatidae (*Carabodes wilmanni*) (after Bellido, 1983).

tematic group of the imago, therefore they are not larvae, but genital organs and furthermore some other structures are lacking. This 'incomplete' situation is not always easy to observe morphologically. However, biological information is useful, because these instars are nearly always unable to live on their own.

The pullus (Pavlovsky, 1924) is an incomplete juvenile instar with special adaptations to life on the mother, such as pad-like organs on the tip of the legs.

The presence of two morpho-biological forms during the same instar among mites is rare amongst the arthropods (except Diptera), but it does not raise any problems of description and does not require any fundamental vocabulary changes; it simply requires more accurate definitions.

Chronological and Morpho-biological Descriptions

In the development of a systematic group of arachnids, except in ricinuleids, pseudoscorpions and perhaps palpigradids, there is no fixed number of instars. Therefore it would be unwise to base a study on few species and to fix the chronology, because some still unknown developments may modify the established system. Theoretical systems of this kind were proposed by Reuter (1909) for mites and by Vachon (1958b) for spiders. Thus, the constant presence of three post-larval juvenile instars (=nymph) in mites stated by Reuter and often followed (protonymphe, deutonymphe, tritonymphe) does not conform to most species,

in which there are less than 3 juvenile instars and even less to those with 4 to 6 instars (e.g. *Ornithodoros maritimus*).

Developmental analyses based on a fixed number of instars (chronological) establishes common points between instars of different species, in order to envisage evolutionary pathways. But these common points will always remain hypothetical, and moreover, these pathways can be elucidated without this system. Therefore we do not wish to use a method with no decisive advantages and, because of its fixed character, limited development descriptions, because species which do not suit the established system are excluded. In mites, for example, the number of instars is considered fixed to one larval, three juvenile instars and the adult. However, in many species one or more juvenile instars are missing and sometimes there are more than three juvenile instars. For mites there is, depending on the species, a variable number of instars.

Evolutionary Pathways

Immature instars of arthropods are adapted to special lifestyles or environments and sometimes differ from those of imagos. Often these adaptations influence the morphology so deeply that it is difficult to distinguish the imago from the immature forms (larva). Such differences are less marked among the arachnids (larvae absent except in mites and ricinuleids).

A good correlate probably exists between the increased level of care by the mother to its clutch and the increased number of incomplete instars at the start of the development.

Moreover, the biology and morphology of early instars can be observed and explained as adaptations to life in the cocoon or with the mother, e.g., the temporary organs such as distal, pedal pad-like organs of pullus (attaching to the mother) or the cheliceral blade of some incomplete juvenile spiders (feeding on undeveloped eggs). The viviparous cases do depend on the same kind of evolutionary processes.

The evolution of many arachnids has probably been characterized by growing care of the clutch correlated with the increasingly and later development of the first instars. Thus, the instars are both incomplete and regressed, because these adjectives depend on the point of view considered: ontogenetic or evolutionary. This corresponds to the 'deux temps' of Grandjean (1954) and, to a certain extent, to the 'state approach' and the 'stase approach' of André (1989).

Mites present great diversity in their biology and, unlike other arachnids, are not all predators. Therefore, they have followed different evolutionary pathways and sometimes metamorphosis takes place, with larvae and nymphs (similar in these cases to those of holometabolic insects) or with 'survival' instars which enable them to disperse.

This evolution of clutch or juvenile care by the mother does not indicate phylogenetic relations in the different orders, because it is a general phenomenon within the animal world and can appear independently in different groups.

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COURTSHIP, MATING AND POST-OVIPOSITION BEHAVIOUR OF *HYPOCHILUS POCOCKI* PLATNICK (ARANEAE, HYPOCHILIDAE)

K. M. CATLEY

Catley, K.M. 1993 11 11: Courtship, mating and post-oviposition behaviour of *Hypochilus pococki* Platnick (Araneae, Hypochilidae). *Memoirs of the Queensland Museum* **33** (2): 469-474. Brisbane. ISSN 0079-8835.

Courtship and mating in *Hypochilus pococki* Platnick is described for the first time for any member of the superfamily Hypochiloidea. Five phases of male behaviour are recognised; pre-courtship, non-contact courtship, contact courtship, copulation and post-copulatory behaviour. Chemotactic stimulation seems to be the prime releaser of male courtship behaviour which involves web-tugging, mutual leg-stroking and female guarding. Post-oviposition behaviour is described and the role of a previously undescribed sheet web, constructed by females after oviposition as well as early instar spiderlings, is discussed in terms of its phylogenetic implications.□*Hypochilus, courtship, phylogenetics, sexual selection, web construction.*

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The significance of undertaking ethological studies of spiders in the family Hypochilidae stems from the phylogenetic position of the family as a relic taxon at the base of the Infraorder Araneomorphae (Platnick, 1977; Forster *et al.*, 1987). Diagnosis of behavioural units that are used in such processes as web construction (Coddington, 1986) and courtship (Platnick, 1971; Helversen, 1976; Coyle and O'Shields, 1990) may prove useful in future phylogenetic analysis. This paper describes the courtship and mating behaviour of *Hypochilus pococki* in the laboratory and attempts to recognise potentially informative behavioural sequences. Egg sac construction is also described and attention drawn to a previously undescribed silk construct, a 'veil web' built by post egg-laying females as well as early instar spiderlings. Apart from one incomplete observation by Fergusson (1972) of mating in *Hypochilus thorelli* Hoffman (=*Hypochilus pococki*), this is the first detailed description of reproductive behaviour for any member of the superfamily Hypochiloidea.

The genus *Hypochilus* comprises five species confined to the Southern Appalachian highlands of eastern North America, two species from central and northern California and one from central Colorado. Two additional species, one from New Mexico and the other from the San Bernardino Mountains of southern California will soon be described (Catley in prep.). These haplogyne cribellate spiders build characteristic 'lampshade' webs on rock surfaces often close to running water. All species appear to be allopatric and exhibit an interesting pattern of disjunct endemism (Catley, 1991; Huff and Coyle, 1992). Males moult to maturity later than females, typically appearing in early August. They move extensively (presumably in search of females) and do not associate with penultimate females, suggesting that there is no first male sperm precedence (Eberhard *et al.* in press).

MATERIALS AND METHODS

Despite extensive day and night observation during 1990 and 1991, no courtship or mating behaviour was observed in the field. *Hypochilus* can be very difficult to maintain in the laboratory; they are affected adversely by changes in humidity and only occasionally can they be persuaded to construct a web, making feeding problematical. Following several unsuccessful attempts to establish a mature female in the laboratory, a single specimen collected in July 1990 from Wolf Creek watershed, Cullowhee, Jackson County NC, established a web in a 50x30cm glass tank. The tank was furnished with a sloping wooden framework (45°angle) covered with sandpaper to simulate an overhanging rock ledge. The floor was covered with vermiculite to a depth of 5cm and was kept very moist.

After the female attacked and killed the first male introduced into the arena, she was allowed to feed for a period of one week. The second male was introduced on August 28 1990 and a total of 7 hours 47 mins of male/female encounters were filmed using a Panasonic WV-D5000 video re-

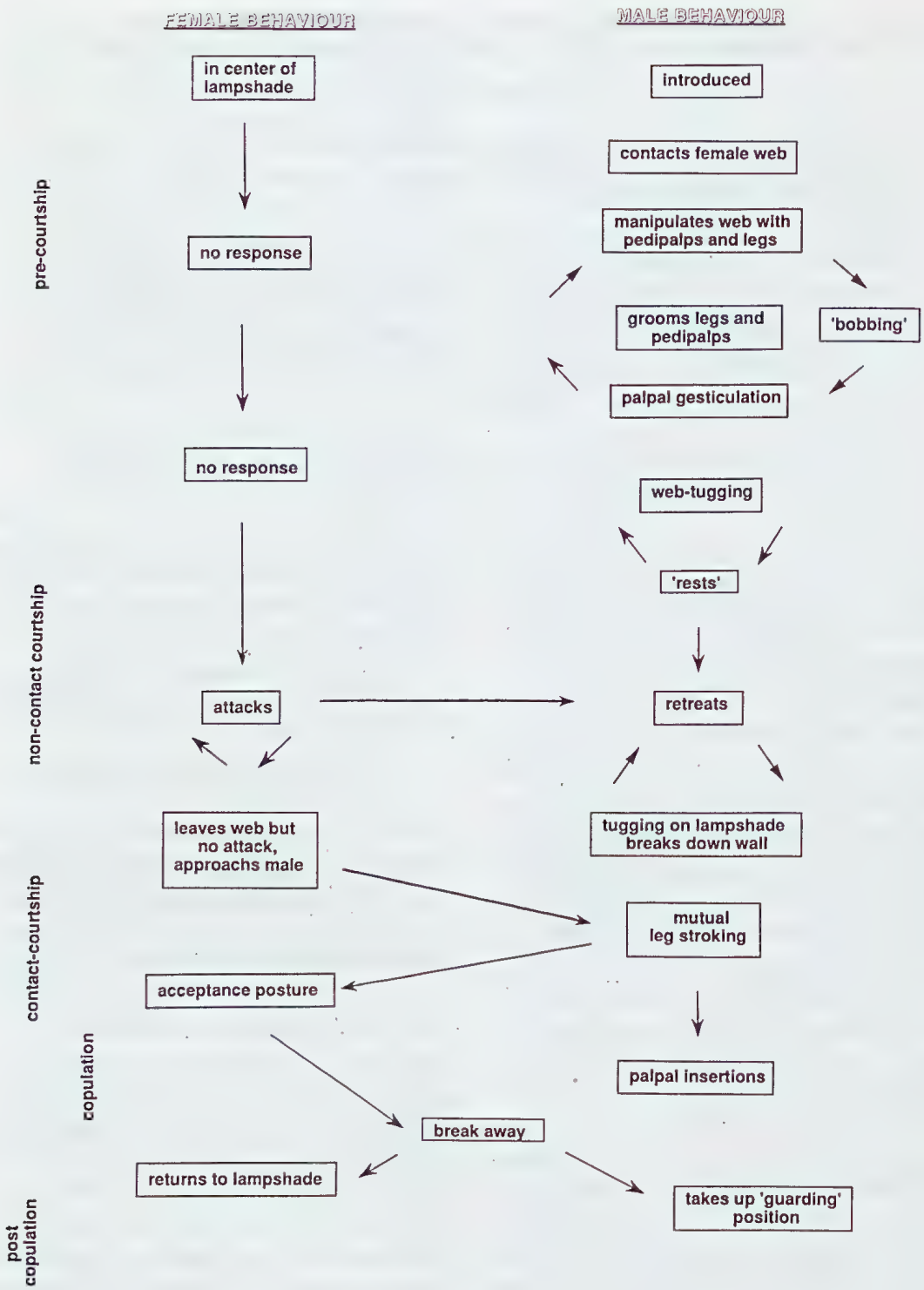

FIG. 1. Sequence of courtship and mating behaviour in *Hypochilus pococki* formulated from encounters in the laboratory involving two males and a single female (see text for explanation).

corder fitted with a Micro-Nikkor 55mm close-up lens. Sessions were annotated by verbal comments recorded through the audio channel of the video camera. Data analysis was achieved using slow motion and freeze frame functions of a VCR.

RESULTS

The description of courtship and mating presented here is a composite derived from laboratory observations of only two males and a single female and therefore may not be representative.

Male courtship behaviour can be divided into five distinct phases: pre-courtship, non-contact courtship, contact courtship, copulation and post-copulation (Fig. 1). The following behavioural units were diagnosed.

Male Behavioural Units

PRE-COURTSHIP

Leg and pedipalpal grooming. Within a few minutes of a male being introduced into the arena, the legs and pedipalps were used to manipulate female silk. A web constructed by the same female but which had been abandoned for several weeks elicited the same response. Rubbing the tarsi and metatarsi of legs 1, 2 and 3 together, as well as drawing them and the pedipalps between the open chelicerae (and presumably the endites) occurred immediately after the first and subsequent encounters with the female web. The pedipalps were rubbed vigorously across the silk for extensive periods, this was followed either by drawing them through the mouthparts, as described above, or by rapid pedipalpal gesticulations.

Bobbing. Flexing of the legs resulted in the whole body moving up and down relative to the substrate. Bobbing is often interspersed between sessions of leg and pedipalp grooming.

NON-CONTACT COURTSHIP

Web-tugging. The male pulled on the cribellate lampshade web of the female with his first pair of legs. Such actions, repeated in bouts lasting 3-7 seconds interspersed with periods of inactivity lasting from 5 secs. to several mins., can result in the side wall of the lampshade being partially destroyed.

CONTACT COURTSHIP

Leg-stroking. The female eventually left the web as a result of male tugging and approached the male, waving her front pair of legs. The male held his ground (unlike previous female approaches which appeared aggressive and from which the male quickly withdrew). A long session of mutual leg-stroking followed, involving mainly legs one and two. The male maintained a constant, very rapid stroking of the female's legs (mainly metatarsi and tibiae) and body as she appeared to become progressively more cataleptic, and eventually assumed the acceptance posture. This stroking session lasted for 3 mins. 12 secs–more than twice the period of copulation itself.

COPULATION

Palpal insertions. Following mutual leg-stroking the female oriented her abdomen at 45° to the substrate and adopted a semi-cataleptic acceptance posture. The male faced the female and advanced, with pedipalps fully extended, to a position where his dorsal cephalothorax was adjacent to the female's sternum (Fig. 2). It was not entirely clear whether or not the male tapped on the female's genital area with his palps prior to insertion as described for some araneids (Robinson and Robinson, 1980). Such apparent tapping may simply be attempts to locate the opening to the bursa copulatrix.

The palps were inserted alternately, the right followed by the left, each insertion lasted 3-10 seconds with the whole insertion sequence lasting 1 min. 22 secs. To achieve insertion from this position requires that the palpal organ be twisted through 90° at the same time as the pedipalp is straightened. The copulatory phase ended abruptly when the female broke away from the male, who was immediately pursued some distance from the web. At no time during courtship or mating was the male observed to lay down silk.

POST-COPULATION

'Guarding' posture. After copulation, the male, after a brief period of palpal grooming, took up a characteristic position close to the female, often touching her. His legs were extended parallel to the substrate, with the first three pair directed anteriorly, and the fourth pair directed posteriorly. The first pair of legs were held in such a position such that the femora were at 30° to the longitudinal axis of the prosoma, while the remaining podites tended to converge distally over the female. This seems to be a characteristic position seen often in the field. It was maintained

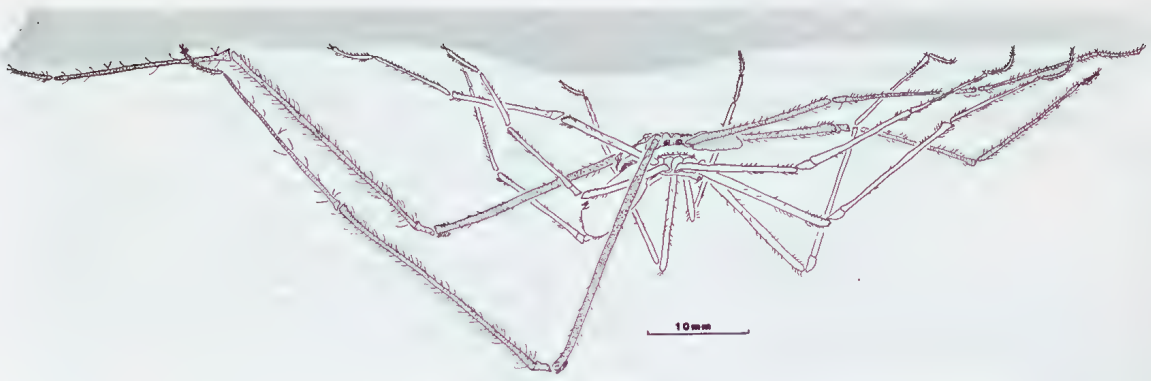

FIG. 2. Mating position of *Hypochilus pococki* (for the sake of clarity not all male appendages are illustrated).

for 2.5 hours after which the female attacked and badly injured the male.

Female Behavioural Units

NON-CONTACT

Attack. The female failed for long periods to show any response to the male's web-tugging but did eventually respond by rushing out of the lampshade and pursuing him. Three attacks appeared in earnest, with the male withdrawing rapidly. The fourth response was instigated more slowly (with reduced speed and vigour); this change in 'intent' appeared to be sensed by the male, who did not retreat. This encounter led directly to contact courtship and copulation (Fig. 2).

CONTACT COURTSHIP

Leg stroking. See male behaviour.

COPULATION

Acceptance posture. A semi-cataleptic position with the abdomen held at 45° to the substrate (Fig. 2) occurring after contact courtship (extensive leg stroking) with the male.

POST-COPULATION

Egg laying ethology. Twenty days after copulation, the female laid eggs and constructed an egg-sac. First a saucer-shaped disc of pink silk was laid down onto which the eggs were deposited. This was then closed up to form a flattened sphere. The pink colour of the silk has been corroborated by several observations in the field, however, when the egg-sac is ready to be covered in cryptic material its colour is off-white. A second egg-sac was produced on October 4, followed by a much smaller egg-sac on October 17, and the final egg-sac was constructed on November 6. Each was suspended from the framelines of the web while particles were incorporated in the outer layer of the egg-sac. This involved the spider descending to the substrate and carrying pieces of vermiculite back to the web in her chelicerae (in the field egg cases are covered with particles of moss or lichen (Fergusson, 1972; pers. obs.).

Two egg-sacs were 'screened in' by a particular type of sheet web not previously described for *Hypochilus*. Observations from the field show that a similar 'veil web' is also constructed by early instar spiderlings (Catley, 1991). The silk is of very different appearance from either framework or cribellate silk and appears as a dense, finely woven sheet. Its purpose, either as a vertical 'veil' in front of egg-sacs (typically those suspended in a fissure in the rock), or as a barrier underneath which a number of very early instar spiderlings build their regular prey catching lampshade webs, may be protective.

DISCUSSION

The function of courtship in spiders may be most simply expressed as: alerting the female to the presence of the male, the possible suppression of female predatory behaviour and stimulation of the female to accept copulation. Variations on this basic theme have been voiced by several authors including Bristowe (1958), Crane (1949) and Platnick (1971); most expand the concept to include elements of species specific recognition, advertisement of sexual availability and the functioning of a releaser system. Other components which may also be important are male behavioural elements designed to ensure his post-copulation survival.

Accounts of courtship and mating in other more primitive spider taxa are scant, but include information on the Mesothelae: Liphistiidae, *Heptathela* (Haupt, 1977); Mygalomorphae: Nemesiidae (Buchli, 1962); Atypidae (Clark, 1969); Dipluridae (Coyle and O'Shields, 1990). Whereas behavioural observations for spiders in the Araneoclada are available from Bristowe (1941, 1958) various families, Crane (1949) for salticids, and Robinson and Robinson (1978, 1980) for araneids, this account of courtship and mating in *Hypochilus* is the first to be published for any lower (non-Araneoclada) araneomorph spider.

The courtship and mating repertoire of *Hypochilus* is relatively underived and given the families' phylogenetic position the behavioural units which comprise it may be hypothesised to represent the plesiomorphic condition of araneomorph reproductive behaviour in general. Given a larger data base within the Araneomorphae, comparison of behavioural characters will allow correct polarity decisions to be made and the resulting data set, combining both morphological and ethological characters, should provide a more stringent test of phylogeny.

Leg and pedipalpal grooming behaviours performed by the male upon contact with the female web may be indicative of the occurrence of female pheromone on the web. Such pre-contact encounters were necessary to release web-tugging behaviour in these observations (n=4) and is consistent with Platnick's (1971) hypothesis that chemotactic stimuli are prime releases of male courtship behaviour in haplogyne spiders. It has been suggested that the longer anterior legs of male *Hypochilus* confer superior mobility when locating females (Fergusson, 1972; Eberhard *et al.* in press). However, such pronounced sexual dimorphism may have had its origin in courtship behaviour. The extreme length of the first legs, by maximising the distance between male and female during web-tugging, should increase the male's chance of surviving female attacks. Such interactions may also provide an opportunity for sexual selection by female choice to occur (Eberhard, 1985), the female testing male 'fitness' by repeated attacks.

Contact courtship was initiated when the female eventually left the lampshade and approached the male. Such behaviour may not however be typical. Fergusson (1972) reported that in the one encounter he observed the male scrambled into the lampshade with the female. The long period of mutual leg-stroking may play a role in placating the female, resulting in her adopting the acceptance posture. It may well be homologous with the 'leg fencing' behaviour seen in some diplurid spiders (Coyle and O'-Shields, 1990).

Copulation was achieved in the mating position (Fig. 2; position 1 of Kaston, 1981). Alternate palpal insertions, as observed in *Hypochilus*, should be considered plesiomorphic when encountered in other araneomorph spiders (using *Hypochilus* as an outgroup) and as apomorphic when palps are inserted simultaneously. Simultaneous palpal insertion has been documented in the following families, Dysderidae, Segestriidae, Oonopidae, Scytodidae and Pholcidae (Bristowe, 1958) but appears not, as Bristowe concluded, to be plesiomorphic for the Araneoclada. Simultaneous insertion may well prove to be a synapomorphy for the higher haplogynes, Dysderoidea plus 'Scytodids' (Coddington and Levi, 1991).

The post-copulatory position taken up by the male is believed to represent a guarding posture. *Hypochilus pococki* males have been shown conclusively not to associate with penultimate females (Eberhard *et al.* in press). Hence, that the numerous occasions when males were found in this position in the field, suggest that they represent in fact, post-mating situations, and that the male was most likely guarding the female and thus his chance of paternity.

The implications of the 'veil' web produced by the female following egg-sac construction require further comment. *Hypochilus* egg-sacs are superbly cryptic and most are not concealed by such a 'veil' web (Shear, 1969; Fergusson, 1972; Catley, 1991). The behaviour of some females in concealing egg-sacs might have primitively represented a selective advantage from vertebrate or hymenopteran predation.

Accepting the cladistic hypothesis of Forster *et al.* (1987) on the relationships of the Hypochiloidea and Austrochiloidea, data on sheet web construction in these taxa suggests that the lampshade web of *Hypochilus* is autapomorphic. *Ectatosticta davidi* (Simon), the sister taxon of *Hypochilus*, constructs a sheet web (Li and Zhu, 1984) as do all known members of Austrochilidae (Forster *et al.*, 1987). Ontogenetic evidence, based on the observation that very early instar spiderlings also construct a sheet web (Catley, 1991), also supports this hypothesis and lends some weight to the suggestion that the plesiomorphic web construct of araneomorph spiders was the sheet web.

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EFFECTS OF SAMPLING METHOD ON COMPOSITION OF A TASMANIAN COASTAL HEATHLAND SPIDER ASSEMBLAGE

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The composition of a spider community in coastal heathlands of north-east Tasmania was derived from a 16 month survey using pitfall traps, sweep net and visual search sampling methods incorporated into a replicated, standardised sampling program. This interpretation of composition is shown to rely on the relative efficiency of the three collecting methods to sample the taxa present. Since mature spiders are required to confirm species identity, the differential selection of age and sex classes by the methods is illustrated. Whilst pitfall traps catch a greater number of taxa (at all taxonomic levels) and adult spiders, certain taxa are not or barely represented by this widely used technique. The subjective nature of the visual search method allows for the potential to target mature spiders. Limits of the sampling methods are emphasised in response to a growing dependence on survey data for the assessment of biodiversity.□*Araneae, methodology, biodiversity, heathland, invertebrates, community.*

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Surveys of spider communities in Australia have primarily been motivated by specific taxonomic interests in this relatively unknown faunal group. Whilst this has lead to invaluable improvements in taxonomy, such collections are increasingly being utilised to extract data for the making of critical conservation management decisions. It is therefore necessary that further consideration be given to the factors that can affect the interpretation of survey results.

The primary factor that limits the comparability of data from different locations or times is the method used to sample spiders. Different methods can preferentially sample certain microhabitats and/or particular taxa (Merrett and Snazell, 1983). For example, the commonly used pitfall trap selects ground active species (Duffey, 1974; Merrett and Snazell, 1983; Lowrie, 1985) and the use of this method alone can produce species lists that under-represent more sedentary or foliage inhabiting members of the community.

The effectiveness of different sampling techniques can be influenced by behavioural differences between not only taxa, but also age or sex classes of a given species. For example, males of many species are more readily captured by pitfall traps than females due to their active search for a mate (Merrett, 1967, 1968), which may represent ground activity in an otherwise foliage dwelling taxa. Since mature specimens are usually required to identify species or genera, the ability to catch adults will effect the accuracy of a species list.

By adopting a suite of collecting techniques to target spiders both on the ground and in vegetation, the chances of sampling all taxa present are increased and thus data more useful for community studies are collected (Uetz and Unzicker, 1976). Accordingly, a combination of pitfall trap, sweep net and visual search methods was selected for a 16 month survey of spiders in the north-east coastal corner of Tasmania. The area is largely developed as sheep and cattle grazing properties, although to the seaward side of the remaining coastal *Eucalyptus* and *Casuarina* forests is often a margin of heathland dominated by members of the Proteaceae, Casuarinaceae, Epacridaceae, Papilionoideae and Xanthorrhoeaceae. An increasing impact of recreational and residential development threatens the remaining heathland (Kirkpatrick, 1977). In this paper, the composition of spiders in the heathland community is inferred by the list of spider taxa collected over the survey period. The relative efficiency of the three sampling methods in capturing dominant taxa is then compared to illustrate how the choice of method can influence the final interpretation of community composition or species richness.

MATERIALS AND METHODS

Spiders were collected using pitfall traps, sweep net and by visual searching, each of which

was standardised for effort and replicated. At monthly intervals from October 1986 to January 1988, sampling was carried out during a one week field trip. Two replicate 90m^2 sites were selected at each of two study areas, Waterhouse Point and Eddystone Point. Within each site there were nine 18m^2 plots placed 18m apart in three rows of three. This allowed for three replicate plots per sampling method, allocated initially at random. For the relevant plot the following sampling routine was employed: a) Nine pitfall traps were set 4.5m apart in a 3 x 3 matrix using 9cm diameter traps; b) one sweep sample of 50 sweeps was taken using a 28cm diameter net in a 12 x 3 m area and c) visual searching for 30 minutes was made over a 3 x 3m area. Spiders were preserved in 70% alcohol, identified to species where possible, and lodged with the Queen Victoria Museum, Launceston, Tasmania.

The three sampling methods were considered to be complementary in their selection of taxa occupying different strata. Pitfall traps sample spiders mobile on the ground, in contrast to sweep netting which targets spiders in the foliage. Visual searching can reveal spiders in any microhabitat, but a bias was shown towards those secured within web retreats, as such groups may not be amenable to capture by the previous two methods.

RESULTS AND DISCUSSION

Composition

A total of 8,625 spiders were collected using all three methods over 16 months, and these spiders comprised 130 species of the Araneomorphae in 97 genera and 34 families (see Table 1). Names could not be allocated to 26% of genera and 92% of species, indicating further that many Australian groups need taxonomic revision (Davies, 1985; Raven, 1988). The most diverse families in terms of the number of species were the Salticidae (14 spp.) and Gnaphosidae (11), followed by the Theridiidae (9), Zodariidae (9), Thomisidae (8) and Araneidae (8). The four most abundant species were, in decreasing order Diaea sp. (5.8%), *Badumna vandiemani* (5.3%), *Odo* sp. (4.3%), *Hestimodema* sp. (4.1%).

The number of spiders falling into pitfall traps depends on their activity (Mitchell, 1963;

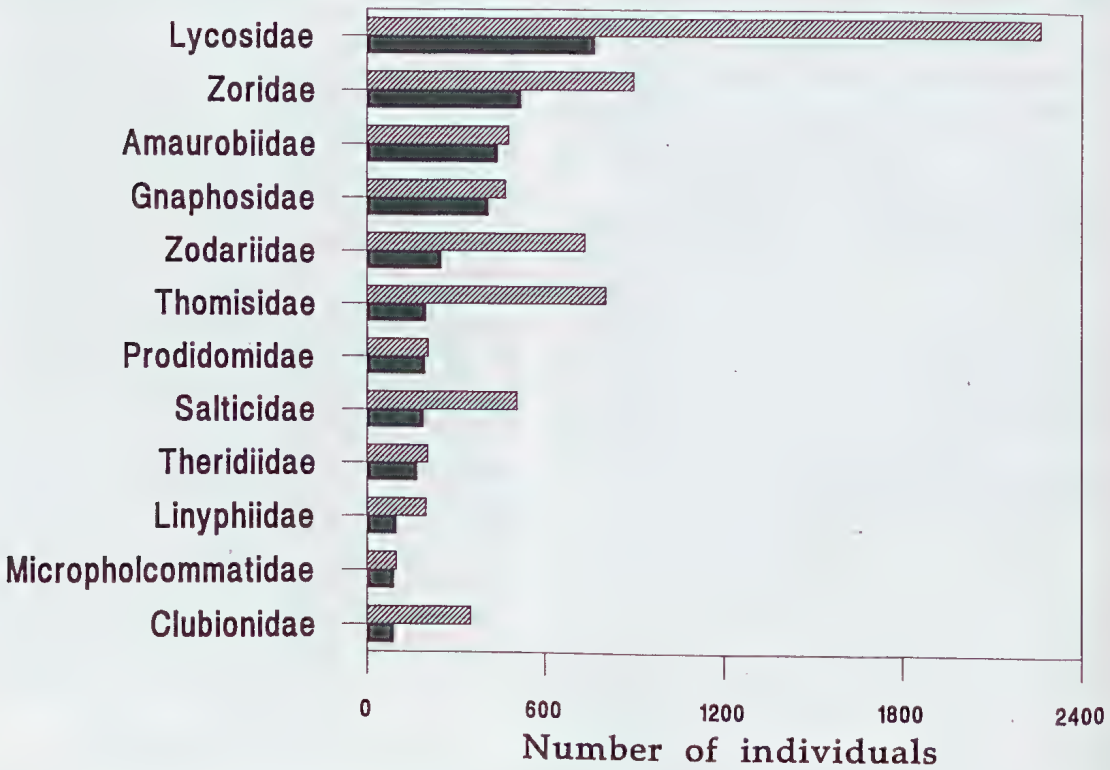

FIG. 1. Number of individuals (shaded bars) and adults (black bars) for the twelve dominant spider families.

Amaurobiidae
Genus A sp.1 *
Genus A sp.2 *
Genus B sp.
Genus C sp.
Genus D sp.

Amphinectidae
Amphinecta milvinus (Simon, 1903)
Mamoea sp.

Araneidae
Cyclosa sp.
Eriophora biapicata (Koch, 1871)
Gasteracantha minax Thorell, 1859
Genus E sp.
Genus F sp.
Genus G sp.
Genus H sp.
Genus I sp.

Clubionidae
Cheiracanthium sp.
Clubiona sp. 1
Clubiona sp. 2
Clubiona sp. 3
Genus J sp.

Corinnidae
Asadipus sp.
Castianeira sp.
Supunna sp.

Cyatholipidae
Hanea sp
Matilda sp.

Desidae
Austmusia sp.
Badumna vandiemani Gray, 1983 *
Forsterina sp.
Tuakana sp.

Dictynidae
Callevophthalmus sp.1
Callevophthalmus sp.2

Gnaphosidae
Anzacia sp.1 *
Anzacia sp.2 *
Eilica sp. *
Megamyrmaekion sp.
Micaria sp.
Trachycosmus sp. *
Zelotes sp.1
Zelotes sp.2
Zelotes sp.3
Genus K sp.
Genus L sp.

Hadrotarsidae
Hadrotarsus sp.1
Hadrotarsus sp.2
Genus M sp.

Hahniidae
Neoaviola sp.

Heteropodidae
Neosparassus sp.

Linyphiidae
Laetesia sp.1 *
Laetesia sp.2
Laetesia sp.3
Laetesia sp.4
Genus N sp.
Genus O sp.

Lycosidae
Artoria sp.1 *
Artoria sp.2 *
Artoria sp.3
Artoria sp.4 *
Artoria spp.
Lycosa funesta (Koch, 1849)
Lycosa speciosa (Koch, 1879)
Lycosa sp.

Micropholcommatidae
Micropholcomma sp.1
Micropholcomma sp.2
Textricella sp.1
Textricella sp.2 *
Textricella sp.3

Mimetidae
Australomimetus sp.

Miturgidae
Miturga sp.1
Miturga sp.2
Uliodon velox (Hickman, 1930)
Uliodon sp.

Mysmenidae
Genus P sp.

Nicodamidae
Nicodamus melanozanthus (Urquhart, 1893)

Oecobiidae
Oecobius annulipes Lucas, 1846

Oonopidae
Orchestina sp.
Genus Q sp.

Oxyopidae
Genus R sp.

Pararchaeidae
Pararchaea sp.

Pisauridae
Dolomedes sp.

Prodidomidae
Molycria sp. *

Salticidae
Lycidas sp.
Maratus sp. *
Opisthoncus sp.
Pseudosynagelides sp.
Servaea sp.
Genus S sp.1
Genus S sp.2
Genus S sp.3
Genus S sp.4
Genus T sp.
Genus U sp.
Genus V sp.
Genus W sp.
Genus X sp.

Stiphidiidae
Biaimi sp.
Corasoides australis Butler, 1929
Stiphidion facetum Simon, 1902

Tetragnathidae
Deliochus sp.
Phonognatha sp.
Tetragnatha sp.

Theridiidae
Achaearanea sp.
Dipoena sp.
Episinus sp.
Euryopis sp.
Phoroncidia trituberculata (Hickman, 1951)
Steatoda sp.1
Steatoda sp.2
Steatoda livens (Simon, 1895)
Theridion sp. *

Thomisidae
Cymbacha sp. *.
Diaea sp. *
Sidymella sp.1
Sidymella sp.2
Sidymella sp.3
Sidymella sp.4
Sidymella longipes (Koch, 1874)
Stephanopis sp.

Toxopidae
Laestrygones setosa Hickman, 1969

Trochanteriidae
Corimaethes sp.

Zodariidae
Asteron sp. *
Asteron "reticulatum"
"Australatica" sp.
Habronestes sp.1
Habronestes sp.2
Habronestes "bradleyi"
Neostorena sp.1
Neostorena sp.2
Nostera sp.

Zoridae
Argoctenus sp.
Hestimodema sp. *
Odo sp. *
Thasyraea sp.

TABLE 1. List of spiders collected from Tasmanian coastal heathlands. Asterisk indicates the 20 most abundant species.

Greenslade, 1964; Uetz and Unzicker, 1976; Merrett, 1983) and not necessarily on actual abundance in the community (Merrett, 1967; Merrett and Snazell, 1983). Individuals active on foliage presumably experience a higher probability of being knocked into a sweep net and for the visual search method the chance of noticing spiders would be increased by their activity (Curtis, 1980). Therefore it is stressed that references to abundance in this paper relate to numbers caught and not population size.

With respect to the number of individuals, the collections were dominated by the Lycosidae (26% of the total), Zoridae (10%), Thomisidae (9%) and Zodariidae (9%) (Fig. 1). The families Salticidae, Amaurobiidae, Desidae and Gnaphosidae then account for the next 22%. With the exception of the zodariids and zorids, these families are amongst the largest in Australia (Raven, 1988). The Araneidae, which are otherwise the most abundant Australian spider family (Raven, 1988), comprised only a minor component of this collection (1.4%).

The dominance hierarchy (Fig. 1) is determined by the number of adults in each family. However, as it is not standardised as to whether the whole data set (including immatures) or only the adult data are used to describe patterns of family dominance in a given community, a comparison is made to both (Fig. 1). The interpretation of relative abundance of families is affected by which category is used. Given that only adult data are useful for comparisons at the generic or species level, adult data seem the better choice for assessments of biodiversity.

Effects of Sampling Method on Composition

Pitfall traps collected the most individuals (6212), followed by visual searching (1900) and sweep netting (513). However, as the sampling effort of pitfall traps far exceeds that of sweep netting and visual searching, comparisons of taxa between methods are made relative to the total of each method.

Due to a reliance on acquiring mature spiders from surveys to confirm species and generic level identifications, Fig. 2 presents the differential distribution of age and sex classes for each sampling method. Pitfall traps clearly caught the greatest percentage of males (35%) and visual searching, the least (3%). Females are also collected more by pitfall traps, although the difference between methods is not as distinct. Accordingly, the percentage of immature spiders increases from pitfall traps (46%), through sweep net (75%) to visual search (84%) methods. From these results pitfall traps seem to be the most efficient at selecting mature spiders from the coastal heathland community.

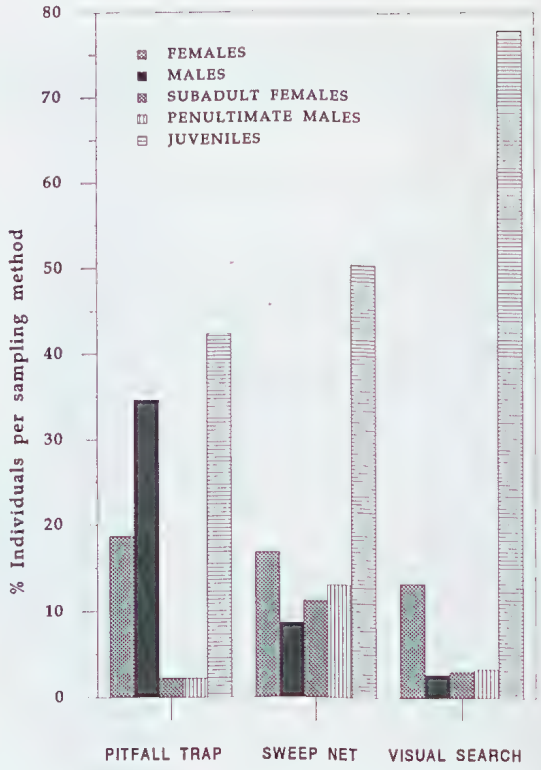

FIG. 2. Percentage of individuals in each sampling method for the different age and sex classes.

The total number of families, genera, and species can be compared to that collected by each sampling method (Table 2). At each taxonomic level, pitfall traps sample the most taxa (between 87-94% of the total), followed by visual searching (41-66%) and sweep netting (25-41%). It is relevant to point out that the results presented here were derived over a 16 month survey period. The likelihood of recording certain taxa using a given sampling method for typically shorter survey periods depends on the relative ease with which they are collected by that method (it also depends on the temporal abundance of taxa, to be discussed elsewhere). The percentage of adult

	Total	Pitfall	Sweep	Visual
Family	34	32	14	23
Genus	97	84	30	45
Species	130	113	33	53

TABLE 2. The number of taxa in total, and for each sampling method at three taxonomic levels.

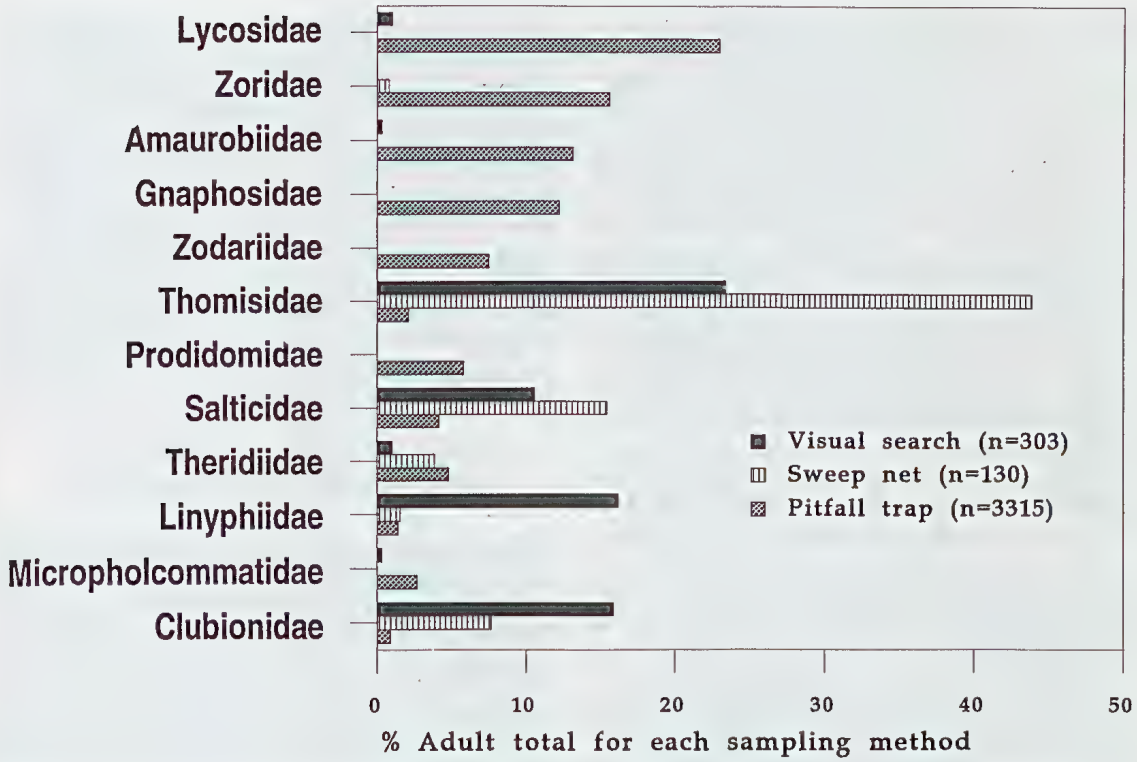

FIG. 3. Percentage of the adult spider total for each sampling method for the 12 dominant spider families.

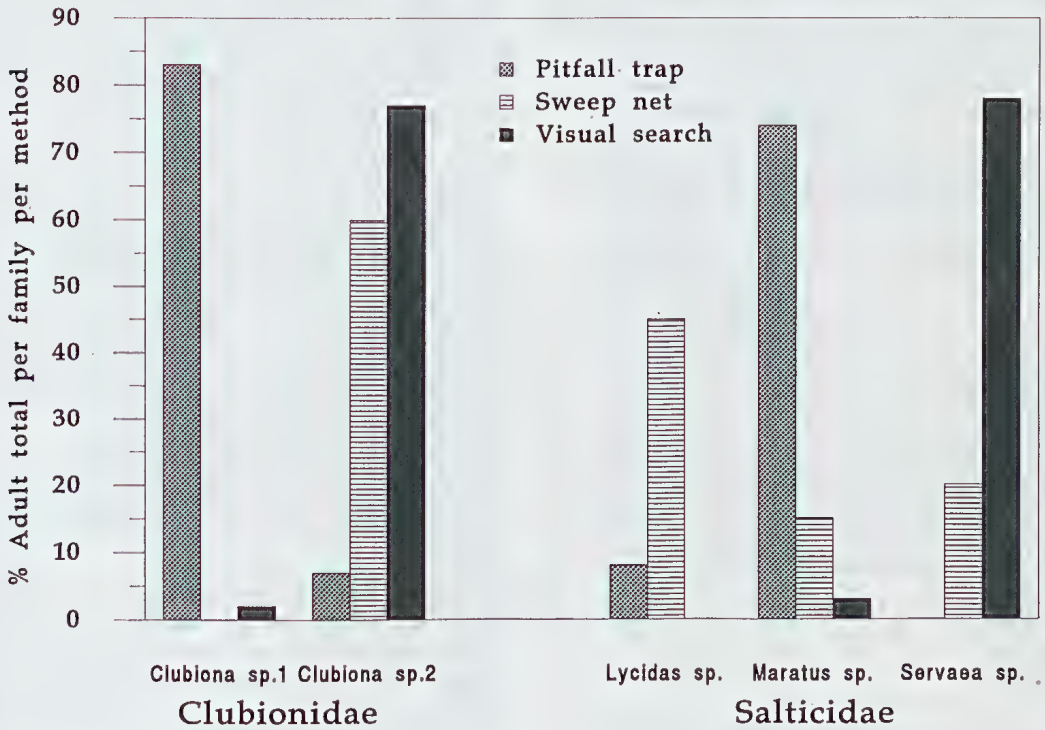

FIG. 4. Percentage of the adult spider total for each sampling method of Clubionidae and Salticidae.

spiders sampled by each method varies over the 12 dominant families (Fig. 3). Ground dwelling spiders such as gnaphosids or zodariids are exclusively caught by pitfall traps. Despite lycosids and zorids being sampled by all methods, there is a reduced chance that they would be represented by sweep net and visual searching over a shorter survey period. If only pitfall traps were used, the probability of representing the families Thomisidae or Salticidae is markedly reduced. Linyphiids, due to their habit of building low webs under the foliage are primarily amenable to capture by visual searching. Consequently, the results show that there is a greater probability of representing some families over others according to the method used.

The number of species in each family are distributed differently across sampling methods (Table 3). Whilst the ground dwelling spiders such as the gnaphosids and zorids have all their species falling into pitfall traps, other families have a pattern of species distribution across methods quite different to the distribution of individuals. For example, thomisids may be best sampled using sweep netting and visual searching (Fig. 3). Yet, these methods inadequately sample all the thomisid species collected (Table 3). The contrast is explained by the two most abundant thomisids, *Diaea* sp. and *Cymbacha* sp. being collected mostly by sweep net and visual search methods. Further examples include all clubionid species being sampled by all three methods (compared to a very unequal distribution of individuals) and a greater number of salticid species being sampled by pitfall traps (compared to this method catching the least number of salticids).

The number of individuals of the dominant species of clubionids and salticids illustrates that the differential selection of taxa by sampling method also operates at the species level (Fig. 4). Within the Clubionidae, despite the two species being collected by all three methods, *Clubiona* sp. 1 was almost exclusively sampled by pitfall traps, whereas *Clubiona* sp.2 was more often taken by a sweep net or visual searching. Similarly, the three dominant salticid species were preferentially sampled by the three different methods. Hence, if one sampling method was favoured over any other, especially for a shorter survey period, many species would be omitted from the final species list.

Family	Total	Pitfall trap	Sweep net	Visual
Amaurobiidae	5	5	0	1
Clubionidae	5	3	3	3
Gnaphosidae	11	11	0	0
Linyphiidae	6	6	1	6
Lycosidae	7	7	0	0
Micropholcommatidae	5	5	0	1
Prodidomidae	1	1	0	0
Salticidae	14	9	7	6
Theridiidae	9	6	2	3
Thomisidae	8	8	2	3
Zodariidae	9	9	0	0

TABLE 3. Number of species in total and for the three sampling methods for 12 dominant families.

IMPLICATIONS FOR THE FUTURE SURVEY OF SPIDER COMMUNITIES

There is currently no spider sampling technique that is unbiased. The success of any method is usually related to certain aspects of spider behaviour and therefore generally represents an incomplete range of taxa. Whilst this may be readily acknowledged by arachnologists, the limitations of a given method is not always clarified in the interpretation of community composition. This is particularly important when non-arachnologists utilise the information as representative of the whole community.

Despite the use of three sampling methods in this survey, the species list is not unbiased. In this study, sweep net and visual search methods were carried out during the day and may therefore not select nocturnally active taxa. Visual searching included looking at the ground, but effective sampling of leaf litter was not undertaken, and this micro-habitat can harbour distinctive families (Raven, 1988). The visual search method is also subjective in terms of where the search focus is directed. Attention was paid in this survey to sample spiders in positions (particularly in nests) that were not as vulnerable to the other two collecting methods. Where the objective of the survey is to estimate taxonomic composition of the spider fauna, the efficiency of both the visual search and sweep net methods could be improved by avoiding the collection of distinctly immature spiders.

Also, the equipment design can effect the number of individuals and taxa caught (eg., for pitfall traps see Luff, 1975 and Curtis, 1980). Temporal factors can further influence which taxa are susceptible to capture by a given method and as discussed by Abraham (1983), this can be related to seasonal migration of spiders between vegeta-

tive strata. To enhance the comparability of survey data, there is therefore a need to standardise methodology, equipment design, sampling effort and timing. Yen and Butcher (1992) also make this plea in respect of terrestrial invertebrate surveys for the ultimate goal of conservation. Methodological limitations need to be taken into account during the final interpretation of taxonomic lists for a more useful assessment of the fauna. These aspects are stressed in the light of a rapidly growing reliance on such data sets for conservation and management in Australia, and the need to critically assess invertebrate survey methods for estimating the loss of biodiversity worldwide (Coddington *et al.*, 1991).

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A NEW SPIDER GENUS (ARANEAE: AMAUROBIOIDEA) FROM RAINFORESTS OF QUEENSLAND, AUSTRALIA

VALERIE TODD DAVIES

Davies, V. Todd. 1993 11 11: A new spider genus (Araneae: Amaurobioidea) from rainforests of Queensland, Australia. *Memoirs of the Queensland Museum* **33**(2): 483-489. Brisbane. ISSN 0079-8835.

Malala gen.nov. is described and its relationships discussed; descriptions of two new species, *Malala lubinae* sp.nov. and *Malala gallonae* sp.nov. are given, including their spigot morphology. *Malala* is considered *incertae sedis* within the Amaurobioidea (*sensu* Lehtinen).□*Araneae, Amaurobioidea, new taxa, spigot morphology.*

Valerie Todd Davies, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 28 October, 1992.

Many amaurobioid spiders in Australia no longer spin a web; they are usually vagrants either in litter or foliage and typically the forelegs have strong ventral spination. Two species of a tree-frequenting genus are described here.

ABBREVIATIONS. Measurements: cephalothorax length (CL) and width (CW), abdomen length (AL) and width (AW). Eyes: anterior median (AME), anterior lateral (ALE), posterior median (PME), posterior lateral (PLE), anterior row (AR), posterior row (PR). Spinnerets: anterior (ALS), median (PMS), posterior (PLS). Collectors: R.J. Raven (RJR), N. Hall (NH), V.E. Davies (VED). *On figures*: **ac** aciniform spigot; **als**, anterior spinneret; **at,** anal tubercle; **c,** conductor; **cp**, protuberance on ♂ chelicera; **cy**, cylindrical spigot; **e**, embolus; **fb**, frontal bristle on ♂ chelicera; **fs,** frontal spur on ♂ chelicera; **Map**, major ampullate spigot; **map**, minor ampullate spigot; **ms**, median sclerite; **n**, nubbin; **pi,** piriform spigot; **pls,** posterior spinneret; **tf**, tegular flange; **to**, tarsal organ. All specimens are lodged in the Queensland Museum.

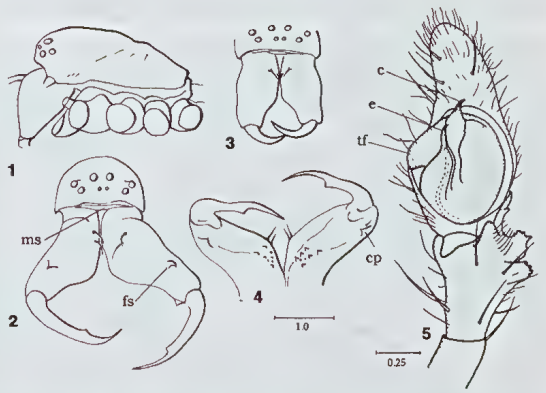
Malala gen. nov.

TYPE SPECIES

Malala lubinae, sp. nov.

DIAGNOSIS

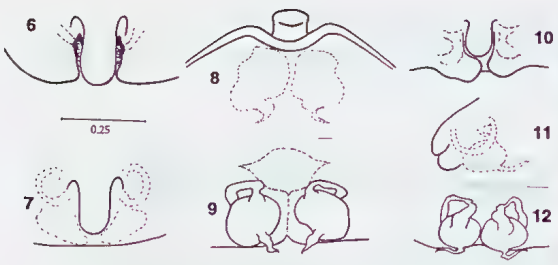
Three-clawed, pale clubionine-like with long spinose legs. Eyes in almost straight rows; AME much smaller than other eyes. Narrow median sclerite above chelicerae. Chelicera with one or two long frontal bristles proximally; pointed frontal spur distally in ♂. ♂ palp without median apophysis; elaborate tibial apophysis with dorso-retrolateral element.



FIGS 1-5. *Malala lubinae*. 1, 3, ♀. 1, cephalothorax (lateral), 3, eyes and chelicerae (frontal), 2, 4, 5, ♂. 2, eyes and chelicerae (frontal), 4, chelicerae (ventral), 5, palp (ventral).

DESCRIPTION

Straw-coloured ecribellate spiders with little or no pattern on abdomen. Carapace rounded dorsally, gradually declining in height behind fovea (Fig. 1). Anterior row of eyes straight, posterior row slightly recurved from above, procurved from front. Canoe-shaped tapetum in indirect eyes. Clypeus x 2 AME; narrow median sclerite above chelicerae (Figs 2,3). Sternum longer than wide, broadly truncate anteriorly, pointed posteriorly. Labium about as wide as long, a little more than half the length of the endite. Four-5 retromarginal cheliceral teeth; proximal ridge leading to 3-5 promarginal teeth, 2 small medial teeth between first and second marginals. Without long retrolateral filamentous setae at base of fang. Legs long (1243), trochanters unnotched. Coxae I longer than IV. Without plumose (ciliate) hairs on body or legs. Numerous strong ventral spines on tibiae and metatarsi I and



FIGS 6-12. *Malala* spp. epigyna. 6-9, *M. lubinae*, ventral, ventral (cleared), posterior, dorsal. 10-12, *M. gallonae*, ventral, lateral, dorsal.

II; metatarsi long, without preening combs; tarsi short. Trichobothria in a single row on metatarsi and tarsi. Bothria grooved, collariform (Fig. 14); tarsal organ with pear-shaped opening (Fig. 13). Superior claws 7-8 teeth, inferior claw 2 teeth; 2 pairs of fringed accessory claw setae present; ♀ palpal claw 2-3 teeth. Colulus. Spinnerets: ALS much larger than PLS; one major ampullate (gland) spigot and nubbin on ALS. Epigynum small with scape-like median structure; anterior gonopores. Male palp with spiniform embolus, membraneous conductor. Tibial apophysis with 3 processes; the anterior process branched or unbranched, the posterior ones 'toothed' and facing each other. Respiratory system with 4 tracheal tubes in abdomen; broad inner tubes branching and rebranching; slender outer tubes simple.

ETYMOLOGY

The generic name is derived from 'malal' an aboriginal word for spider.

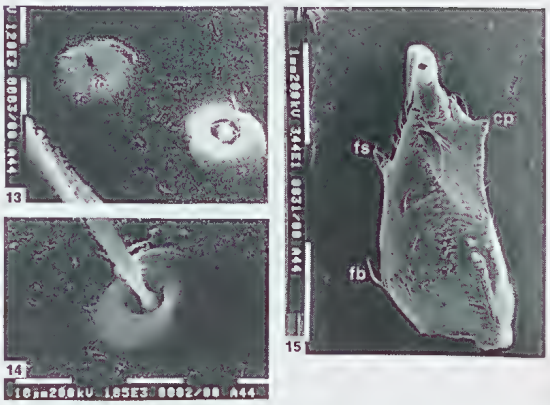
Malala lubinae sp. nov.
(Figs 1-9, 13-17, 20-27)

MATERIAL EXAMINED

TYPES. Lamington National Park, southeastern Queensland. Holotype: ♀, Nagarigoon, 8.iv.1976, VED, NH, S20349. Paratypes: Nagarigoon, 1 ♂, 8.iv.1976, VED, NH, S20350; 4 ♀, 2 j, S20351; Binna Burra, 1 ♂, 1 ♀, 27-30.iii.1976, RJR, VED, S20352; 5 ♀, 11-12.ii.1981, Y. Lubin, RJR, VED, S20353; 1 ♀ with spiderlings in sealed leaf, S20354; Mt Hobwee, 1 ♀, 3-8.iv.1976, RJR, VED, S20355; O'-Reillys, 1 ♂, 15-16.xi.77, VED, E. Dahms, S20356.

DESCRIPTION

Female: CL 3.6, CW 2.6, AL 3.8, AW 2.5. Ratio of AME:ALE:PME:PLE is 4:10:9:10; width of AR is 21, PR is 25. Sternum longer than

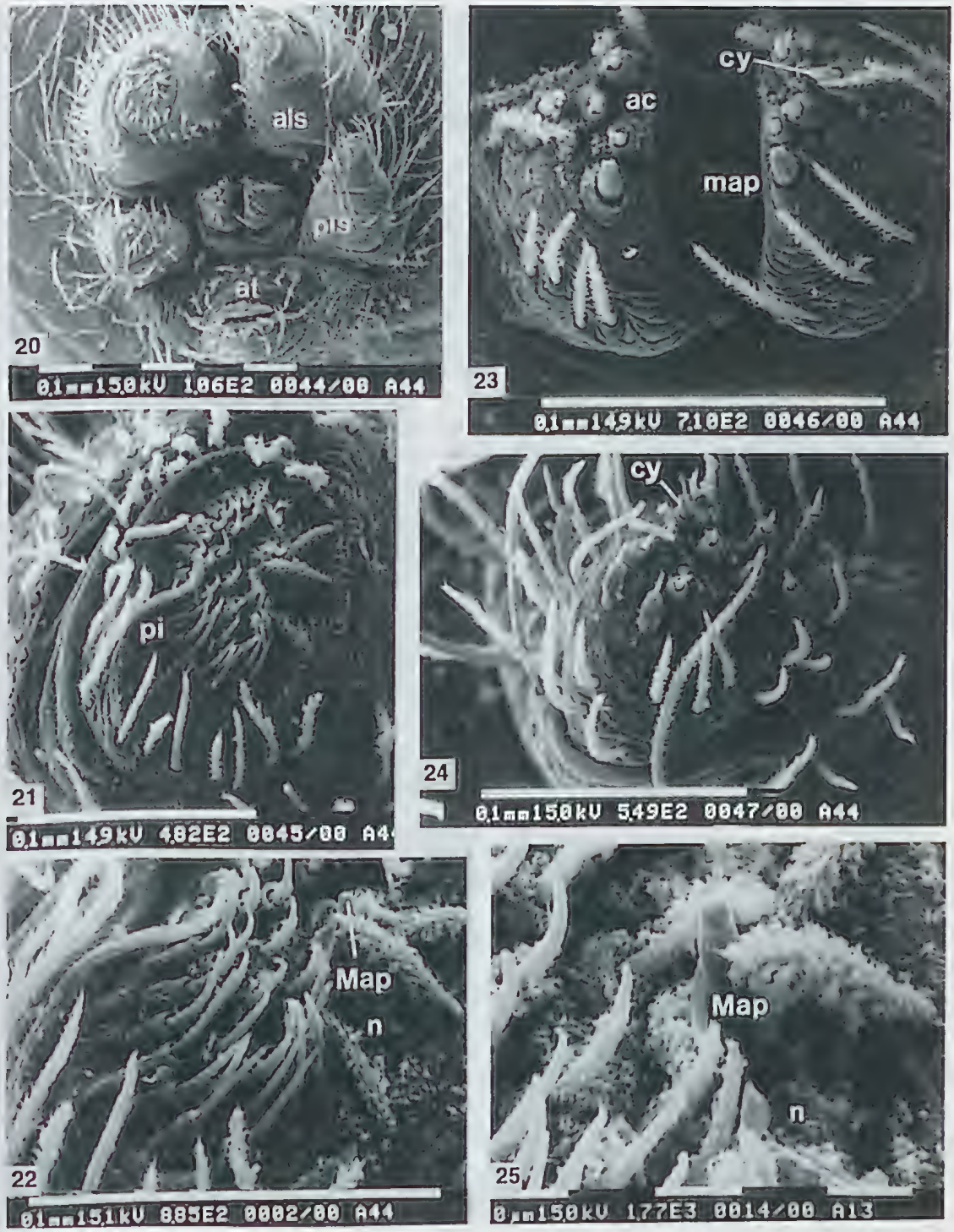


FIGS 13-15. *Malala lubinae*. 13, tarsal organ and bothrium, 14, trichobothrial base, 15, ♂, chelicera (prolateroventral).

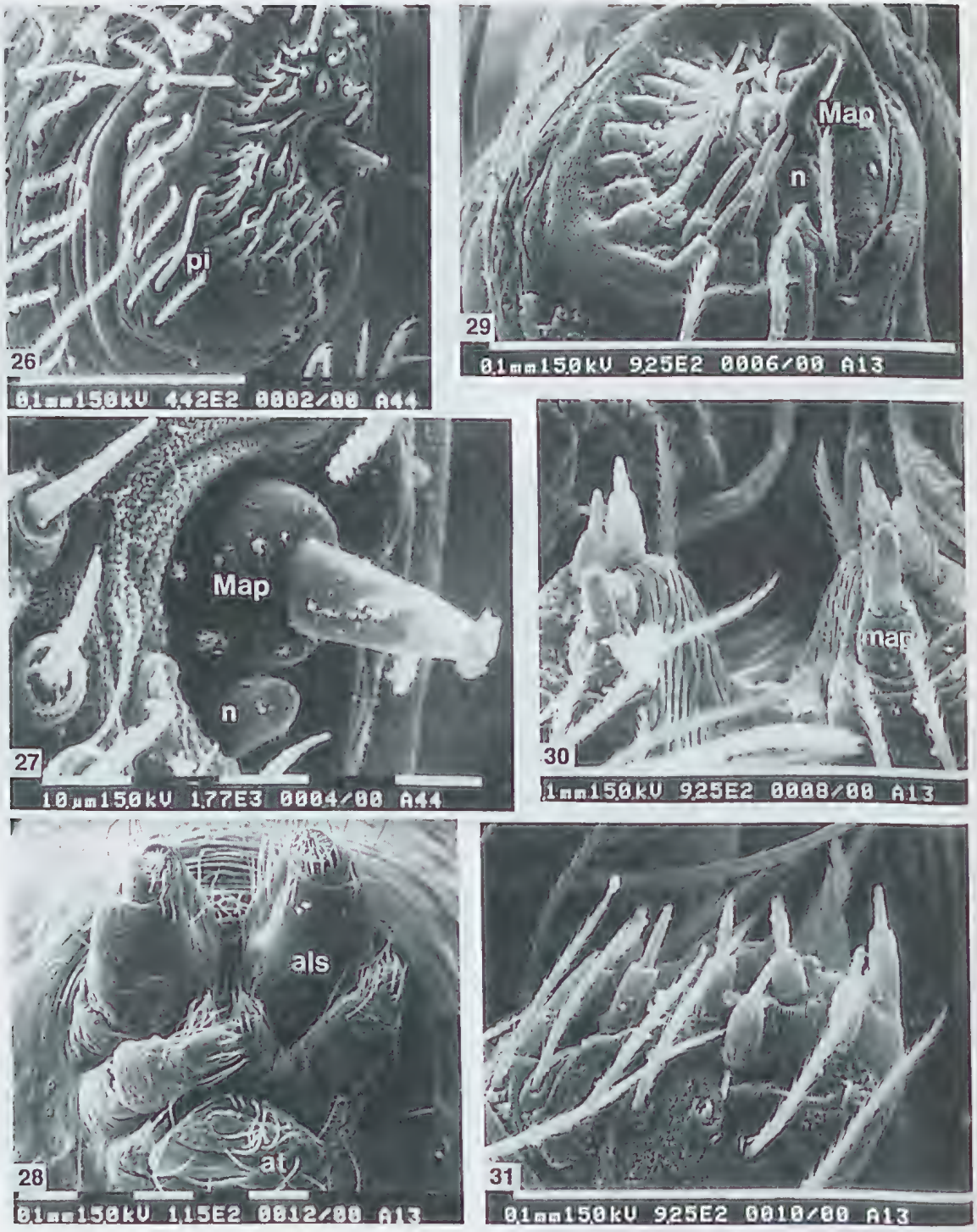
wide 1:0.8; endite 1:0.6. Chelicera with 5 retromarginal teeth and 5 promarginal; second proximal tooth largest. Chelicera with 2 stout frontal bristles; low retrolateral swelling near base of fang; fang with slight ventral projection. Length of coxae I:IV is 1:0.6. Leg measurements are given in Table I.

Notation of spines. Femora: palpi, D0-1-1; I, D1-1-1, PO-0-2, RO-0-2; II, D1-1-1, PO-1-2, R0-1-1; III, D0-1-1, PO-2-1, RO-1-1; IV, D1-1-1, PO-0-1, R0-0-1. Patellae: palpi, D0-0-1; Tibiae:

FIGS 16-19. ♂ palps. 16, 17, *M. lubinae*. 16, left palp, 17, tibial apophysis. 18, 19, *M. gallonae*. 18, left palp, 19, tibial apophysis.



FIGS 20-25. ♀ *M. lubinae* spinnerets. 20, spinneret group. 21, 22, 25, right ALS. 23, PMS. 24, right PLS.



FIGS 26-31. *Malala* spp. spinnerets. 26, 27, penultimate ♀ *M. lubinae*. 26, right ALS, 27, major ampullate spigot and nubbin on ALS. 28-31 ♂ *M. gallonae*. 28, spinneret group, 29, right ALS, 30, PMS, 31, left PLS.

palpi, D1-0-1, P1-1-0; I, P2-1-1, V7-6-2, R1-1-1; II, P2-1-1, V5-5-1, R1-2-0. III, P2-1-0, V2-1-2, R2-1-0; IV p1-1-1, V1-1-2, R1-1-1. Metatarsi: I, P2-2-1, V4-3-1, R1-1-1; II P2-1-1, V4-2-3, R1-1-2; III, D2-2-2, P1-0-1, V2-2-1, R1-0-1; IV, D2-2-2, P1-0-1, V2-2-1, R0-1-1. Tarsi: palpi, P2-1-0, V0-0-2. Palpal tarsi swollen distally. Dorsal abdomen with slight foliate pattern. Epigynum very small (Figs 6-9).

Spinnerets: ALS much larger than PLS (Fig. 20). ALS with one large major ampullate spigot (Map), a nubbin (n) and about 30 piriform (pi) spigots arranged in 2 groups (Figs 21, 22, 25). The major ampullate spigot and nubbin are shown more clearly in a penultimate female (Figs 26, 27). PMS (Fig. 23) with large minor ampullate spigot (map), 3 aciniform gland spigots (ac) and one cylindrical gland spigot (cy). PLS (Fig. 24) with one large cylindrical spigot and 10 aciniform spigots.

Other females varied in size: CL 2.9-3.9, CW 2.3-2.9, AL 3.5-4.4, AW 2.3-2.8.

Male: CL 3.1, CW 2.3, AL 3.3, AW 2.0. Ratio of AME:ALE:PME:PLE is 5:9:8:9. Chelicerae divergent; 2 stout setae (fb) crossing over frontally with lesser one above; pointed spur (fs) distal to these. Four teeth on retromargin of chelicera, 4 on promargin; conical protuberance (cp) near base of fang; fang long with marked ventral projection (Figs 2,4,15). Length of coxae I:IV is 1:0.7. Leg measurements are given in Table I.

Notation of spines: Femora: palpi, D0-1-1; I, D1-1-1, P0-0-2, R0-1-1, II, D1-1-1, P0-2-1, R0-1-2; III, D0-1-1, P0-1-1, R0-1-1; IV, D1-1-1, P0-0-1, R0-0-1. Patellae: palpi, D0-0-1. Tibiae: I, P2-1-1, V7-4-1, R1-1-1; II, P2-1-1, V6-4-1, R1-1-1; III, P2-1-0, V2-1-2, R1-1-1; IV, P2-0-1, V1-1-2, R1-1-1. Metatarsi: I, P2-1-1, V4-2-2, R1-1-1; II, P2-1-1, V3-3-2, R1-1-1; III, D0-1-1, P2-0-1, V3-2-2, R1-1-1; IV, D0-1-1, P1-1-1, V2-2-2, R1-1-1.

♂ palp (Figs 5,15): tegulum extended to form anterior prolateral flange; embolus, arising ventrally on tegulum, tapers to a point; conductor membraneous with pointed sclerotized tip; cymbial tip shorter than length of tegulum. Tibia with 3 retrolateral processes, the anterior one branched.

Variation in size: CL 3.1-3.3, CW 2.4-2.5, AL 3.6-3.8, AW 2.1-2.2.

Biology

The spiders were collected from branches or foliage of trees in the rainforest. The egg sac was placed with the spider in a sealed portion of the prickly leaf blade of *Calamus muelleri*, the lawyer vine.

Malala gallonae sp. nov.
(Figs 10-12, 18, 19, 28-31)

Material Examined

TYPES. Holotype: ♀, Bellenden Ker Range, 1054 m, 17.x-24.xi.1981, Earthwatch/ Queensland Museum Expedition, S20357. Paratypes. Same data as holotype; 1 ♂, S20358, 1 ♀, S20359; 1 ♀, S20360. 1 ♂, same locality, 25-31.x.1981, S20361. 1 ♂, Malaan State Forest,, 20-4.iv.1978, RJR, VED, S20362. Upper Boulder Creek, 11km NW Tully, 850-1000m, 1 ♀, 17-18.xi.1984, J. Gallon, VED, S20363; 1 ♀, S20364; 1 ♂, 6.xii.89, G.B. Monteith, S20365. All in northeastern Queensland.

Female: CL 2.7, CW 2.0, AL 3.2, AW 1.9. Ratio of AME:ALE:PME:PLE is 4:8:9:8. Chelicerae with single stout elongate frontal bristles crossing each other. Four retromarginal, 3-4 promarginal teeth on chelicerae. Fang with slight ventral projection. Length of coxae 1:IV is 1:0.8. Leg measurements are given in Table 1.

Notation of spines: Femora: palpi, D0-0-1; I, D1-1-1, P0-2-1, R2-1-2; II, D1-1-1, P0-2-1, R1-2-1; III, D0-1-1, P0-2-1, R0-2-1; IV, D1-1-1, P0-0-1, R0-0-1. Patellae: palpi, D0-0-1. Tibiae: palpi, D1-0-1, P2-1-0; I, P2-1-1, V6-5-1, R2-1-1; II, P2-1-1, V5-5-1, R2-1-1; III, P2-1-0, V0-2-0, R1-2-0; IV P1-1-0, V0-1-0, R1-1-0. Metatarsi: I, P2-1-1, V4-2-3, R1-1-2; II, P2-1-1, V4-2-2, R2-0-1; III, D2-2-2, P1-0-1, V2-2-1, R1-0-1; IV D2-2-2, P1-1-1, V2-2-1, R0-0-1. Epigynum (Figs 10-12).

Variation in size: CL 2.6-2.8, CW 2.0-2.1, AL 3.0-3.4, AW 1.8-2.5.

Male: CL 2.4, CW 1.8, AL 2.9, AW 1.4. Ratio of AME:ALE:PME:PLE is 4:8:9:8. Chelicerae slightly divergent; single enlarged setae crossing over frontally, pointed spur distally; without protuberance near base of fang. Three retromarginal, 4 promarginal teeth. Leg measurements are given in Table 1. Notation of spines is similar to ♂ *M. lubinae*.

♂ palp (Figs 18,19): tegulum without prolateral flange, embolus arising prolaterally. Cymbium tip a little shorter than length of tegulum. Tibia with 3 retrolateral processes, the anterior one with 2 branches.

Spinnerets: ALS (Fig. 29) have a large major ampullate spigot, a nubbin and about 20 piriform spigots. PMS (Fig. 30) have a large minor ampul-

TABLE 1. Leg measurements (mm) of *Malala* spp. *Bowed.

Leg	Fe	Pa	Ti	Me	Ta	Total
M. lubinae						
♀ palp	1.5	0.5	0.9	-	1.3	4.2
I	3.5	1.2	3.9	3.1	0.9	12.6
II	2.7	1.2	3.0	2.6	0.8	10.3
III	2.0	1.0	1.6	2.0	0.7	7.3
IV	2.6	1.0	2.3	2.9	0.9	9.7
♂ palp	1.5*	0.5	0.7	-	1.2	3.9
I	3.2	1.2	3.7	3.1	1.0	12.2
II	2.5	1.0	2.8	2.5	0.9	9.7
III	1.9	0.8	1.2	1.8	0.7	6.4
IV	2.3	0.9	2.1	2.5	0.8	8.6
M. gallonae						
♀ palp	1.1	0.5	0.7	-	1.0	3.3
I	3.1	1.0	3.6	3.1	0.9	11.7
II	2.6	1.0	2.9	2.6	0.8	9.9
III	1.8	0.8	1.5	1.9	0.6	6.6
IV	2.3	0.8	2.0	2.5	0.8	8.4
♂ palp	1.1	0.4	0.5	-	1.2	3.2
I	2.9	1.0	3.9	3.1	0.9	11.8
II	2.5	0.9	2.7	2.5	0.8	9.4
III	1.8	0.7	1.3	1.8	0.6	6.2
IV	2.0	0.7	1.8	2.3	0.7	7.5

late spigot and 3 aciniform spigots. PLS (Fig. 31) have 10 aciniform spigots.

Variation in size: CL 2.0-2.8, CW 2.0.

DISCUSSION

Malala, a 3-clawed ecribellate, has a single row of tarsal trichobothria of increasing length distally and a single row of metatarsal trichobothria. The ♂ palp has a complex tibial apophysis and no median apophysis. The ♂ chelicerae diverge distally and have a pointed frontal spur distally. The median tracheal trunks are branched. The anterior lateral spinnerets have one major ampullate gland spigot and a nubbin. From these and other characters *Malala* clearly belongs in the amaurobioid/dictynoid complex of families. In his world revision of cribellates, Lehtinen (1967) recognised one major superfamily Amaurobioidea with 6 families. Describing New Zealand spiders, Forster (1970) and Forster and Wilton (1973) defined two groups, Dictynoidea and Amaurobioidea, based on the branching or non-branching respectively of the median tracheal trunks. However, Gray (1983) found that *Forsterina*, an acknowledged close relative of *Badumna* (classified by Forster and Wilton in Desidae: Dictynoidea) has simple median trunks thus invalidating the branching as a synapomorphy for the dictynoids. Gray's evidence suggests that the branching may be important only at the generic level in the same way as the extension of the trunks into the cephalothorax is regarded. In their recent paper on the higher systematics of Araneae, Coddington and Levi (1991) state that 'these superfamilies are among the largest cladistic problems at the family level' and that the difficulty of definition 'partly stems from heterogeneity within families'. I would add that the few Australian genera on which some of these families are based compared with the large number yet to be described, also contributes to this difficulty.

Most Australian rainforest cribellates which range in size from small to very large have a nondescript but recognisable abdominal pattern (see Lehtinen, 1967: 435), a divided cribellar field, a single row of tarsal trichobothria increasing in length distally and a row of metatarsal trichobothria. The ♂ palp has a complex tibial apophysis and a median apophysis is usually present. I am persuaded to return to Lehtinen's classification and regard these Australian spiders as belonging in the Amaurobioidea.

Only one dictynid, *Callevophthalmus* is described from Australia. It is found in grassland and open forest and not, so far as I know, in rainforest. It is a small spider with a distinct abdominal pattern and an entire cribellar field. It has no tarsal trichobothria and a single metatarsal trichobothrium. The ♂ palp has a small tibial apophysis, a large T-shaped conductor extending beyond the edge of the cymbium retrolaterally and has no median apophysis. The ♂ chelicerae are indented prolaterally and have a proximal frontal process; these modifications do not appear to be homologous with those of *Malala*. *Callevophthalmus* is similar to *Arangina* from New Zealand and to *Dictyna*.

This is the first description of spigot morphology in an ecribellate amaurobioid. In general, cursorial spiders use silk only as a drag-line, and for the construction of the cocoon in the ♀. Thus, it is expected they will have fewer kinds of spigots than the web-spinning (cribellate) amaurobioids. *Malala* has 3 aciniform spigots on the PMS and 10 on the PLS. The typical small aciniform spigots which provide silk for swathing prey (Kovoor, 1987) are not present in *Malala*. The lack of these in contrast to their abundance in cribellate amaurobioids and dictynoids (Coddington, 1990b) is probably associated with

Malala's nomadic existence. The presence of one major ampullate gland spigot (Map) and a nubbin on the ALS is found in dictynoids (notably in *Dictyna*) and in the Orbiculariae (Coddington, 1990a) as well as in some other taxa (Platnick *et al.*, 1991). The nubbin (presumably a remnant of a second major ampullate spigot) may be homoplasious in *Malala*.

The fringed accessory claw setae present in *Malala* are probably an adaptation to tree- or foliage-dwelling and are similar to those found in some New Zealand spiders (Forster, 1970; figs 28-31) from a similar habitat. They are unlike the serrate setae which are involved in handling silk in araneoids. The presence of a narrow median sclerite above the chelicerae in *Malala* may be apomorphic. Marples (1962) mentions that a triangular sclerite is present in *Matachia* but not in *Paramatachia*.

At present I am unable to place *Malala* in a family and consider it *incertae sedis* within the Amaurobioidea (*sensu* Lehtinen).

ACKNOWLEDGEMENTS

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AN INVENTORY OF THE SPIDERS IN TWO PRIMARY TROPICAL FORESTS IN SABAH, NORTH BORNEO

CHRISTA L. DEELEMAN-REINHOLD

Deeleman-Reinhold, C.L. 1993 11 11: An inventory of the spiders in two primary tropical forests in Sabah, North Borneo. *Memoirs of the Queensland Museum* 33(2): 491-495. Brisbane. ISSN 0079-8835.

Collecting trips were made to a primary rainforest area at 1500-1900m altitude (Mt Kinabalu National Park) and a primary lowland rainforest (Danum Valley Field Centre) in Sabah, North Borneo. For comparison, a strongly degraded secondary forest in the town Kota Kinabalu was also sampled. All the material, with the exception of the mygalomorphs and salticids, has been identified and compared with collections from Sarawak, Kalimantan and Sumatra. 254 species were distinguished in approximately 120 genera, 35 could be identified as known species, seven of which were clearly synanthropic, the rest are undescribed. 207 species were found in one locality only: 85% of the species from Kinabalu, 70% of the species of Danum and 50% of the species from the town park. Widespread species were found mainly in the Araneidae, Pholcidae, Oonopidae, Clubionidae and Salticidae. A list of the genera and species is given. □*Biodiversity, rainforest, Asia, Araneae.*

Christa L. Deeleman-Reinhold, Sparrenlaan 8, 4641 GA Ossendrecht, The Netherlands; 8 April, 1993.

Tropical rainforests, covering only 6% of the Earth's surface, are believed to harbour more than half of all terrestrial animal species, of which less than 10% are described at present (Stork and Gaston, 1990). Inventorying the spider fauna of rainforests in south-east Asia has given spider taxonomy a new turn, especially so after the introduction of a new sampling method that targets canopy arthropods.

Most rainforests in Asia have now been destroyed or degraded, but the number of undescribed species is still overwhelming. The rapid destruction of our rainforests is an incentive to securing as much data as possible as ... 'an extensive program of inventorying aimed at estimating diversity of species ... is essential for a fuller understanding of the role of biodiversity in ecosystem function' (Coddington *et al.*, 1992).

Records of spiders from Borneo are extremely poor. With more than 30,000 species of spiders described so far, only about 160 named spider species have been described or recorded for the whole of Borneo; 65 of these are salticids. Only 96 spider species were reported from Borneo before World War I. Wanless and Hillyard (1984) present a list of species collected during the arachnological survey of Gunung Mulu National Park, Sarawak; 360 species were collected in all families, 38 of which were identified with known species, another 14 with reserve; 20 identified species are salticids. From Sabah, a mere 20 spider species are known, all published since 1979 (Deeleman-Reinhold, 1980, 1987; Lehtinen, 1979, 1981, 1982; Levi, 1982, 1983; Okuma, 1988; Platnick and Murphy, 1984; Wanless, 1987).

In a privately undertaken program of inventorying spiders of primary and secondary forests in south-east Asia, during the last 14 years I have been engaged, with the help of other, partly autochthonous collectors, in surveying the spider fauna of south-east Asia, mainly Indonesia, Malaysia, Thailand, Sri Lanka and the Philippines. As part of this initiative, I made three collecting trips to Sabah in the north-eastern part of Borneo.

METHODS

In June 1979, July 1980 and April-May 1991, I collected spiders in the primary rainforest of Mount Kinabalu National Park at altitudes of 1500-1900m. In May 1991, 2 days were spent collecting at an altitude of 500m (Poring Hot Springs). In May 1991, spiders were collected in lowland primary forest around the Danum Valley Field Centre in eastern Sabah. For comparison, some time was also spent collecting in the town park in Kota Kinabalu.

The spiders were collected by hand picking, sweeping, litter sieving and pitfall trapping on the ground. All araneomorph spiders, with the exception of the Salticidae have been identified (Tables 1-3). The collected spiders were compared with most specimens of the above mentioned south-east Asia collection. Identification was done as

Oonopidae
Dysderina sp. (1)
Gamasomorpha sp. (2), Sabah
sp. (2)
Ischnothyreus sp. (4)
Opopaea ? (1)
Orchestina sp. (1)
sp. (1), Sabah, only below 600m
Plectopilus sp. (1)
Xyphinus lemniscatus Deeleman
sp. (1), *
Undescribed genus (1), also lower in secondary forest
Tetrablemmidae
Ablemma
Borneomma
Sabahya
circumspectans Deeleman, also lower in secondary forest
roberti Deeleman
kinabaluana Deeleman
bispinosa Deeleman
sp. (1)*
Ochyroceratidae
Psiloderces sp. (1)
Speocera sp. (1)
Undescribed genus (1)
Scytodidae
Scytodes pallida Doleschall, widespread*
Pholcidae
Uthina sp. (1), Sabah
sp. (1)*
Spermophora sp. (1), Sabah
miser Bristowe, widespread*
Belisana sp. (1)
Undescribed genus (1)
Heteropodidae
Heteropoda sp. (1)
sp. (1)canopy walk*
Thelcticopis sp. (1)
Olios sp. (1)*
Undescribed genus (1), in grass
Undescribed genus (1), canopy walk*
Ctenidae
Ctenus sp. (1)
Clubionidae s.l.
Clubioninae
Cheiracanthium sp. (1)
Clubiona sp. (4)
sp. (1) canopy walk*
sp. (1)widespread
Phrurolithinae
Otacilia sp. (1), also at 500m
Sesieutes sp. (1), Sabah
sp. (1)
Teutamus sp. (1)
Orthobula sp. (1), Sabah
Corinninae
New genus (1)
Gnaphosidae
Jacaena sp. (1), on the lawn
Palpimanidae
Boagrius sp. (1)
Zodariidae
Asceua sp. (1)
sp. (1)*
Malinella sp. (3)
Undescribed genus? (2)
Thomisidae
Borboropactus sp. (1)
Lycopus sp. (1), also at 500m
Misumenops sp. (1), canopy walk*
Pagida sp. (1)
Phrynarachne sp. (1)
Oxyopidae
Oxyopes sp. (1), canopy walk*
Pisauridae
Polybaea sp. (1)
Lycosidae
Pardosa sp. (1)
Undescribed genus (1)
Hippasinae (1)
Hahnidae
Alistra sp. (1)
Hahnia (2)
Hersiliidae
Hersilia sp. (1)
Theridiidae
Achaearanea mundula (L. Koch), widespread
tepidariorum (C.L. Koch), worldwide
sp. (1)
spp. (3)*
Anelosimus sp. (1), canopy walk*
Argyrodes xiphias Thorell, widespread
Rhomphaea sp. (1)
Chrysso sp. (1)
Coleosoma sp. (2), Sabah
Coscinida sp. (1)
sp. (1)*
Dipoena sp. (5)
sp. (1)*
Episinus sp. (2)
Janula sp. (1), Sabah
Meotipa sp. (1)*
Phoroncidia sp. (2), Sabah
sp. (1)*
Theridion sp. (4)
spp. (3)*, 1 on canopy walk
Undescribed genus (2)
sp. (1), also at 500m
Undescribed genus (1)
Mimetidae
Mimetus sp. (3)
Theridiosomatidae
Plato sp. (1)
Theridiosoma sp. (1)
Mysmenidae
Undescribed genus (1)
Tetragnathidae
Leucauge celebesiana Walckenaer, widespread
spp. (2), Sabah
Glenognatha sp. (1)
Mesida sp. (4)
Undescribed genus I (2)
Undescribed genus II (2), also at 500m
Undescribed genus III, (1), also at 500m
Araneidae
Araneus sp. (1)
Argiope reinwardtii Doleschall, widespread
aemula (Walckenaer), widespread
Cyclosa bifida Doleschall, widespread
Cyrtophora sp. (1)
? Eriophora sp. (1)
Gasteracantha sp. (1)*
Milonia brevipes Thorell, widespread
Neoscona nautica L. Koch, world tropics
Undescribed genus (1)
Linyphiidae
Neriene beccarii Thorell, widespread
Kuala sp. (1)
Parameioneta sp. (1)
Nasoona sp. (3)
sp. (1)*
Undescribed genus II (1)
Undescribed genus III (1)
Undescribed genus IV (1)
Undescribed genus V (2)
Uloboridae
Philoponella sp. (1)
Uloborus lugubris Thorell, widespread*
Psechridae
Psechrus kinabalu Levi

Table 1. Spiders from Mount Kinabalu, 1500-1900m (Headquarters and Power Station) and 500m (Poring Hot Springs), primary rainforest, 18 collecting days in April-May, June and July. Family order is 'phylogenetic'. List gives no. of undescribed species in parentheses and notes on species.*= only at 500m.

much as possible with the aid of modern revisions but, where these do not exist, I had to rely on the keys in Simon (1892-1903) and the Latin descriptions (without illustrations) of Thorell (1877-1899) and Simon. Many nineteenth century types deposited in Genova, Paris and London were studied. Only species of which adults were collected are considered here.

RESULTS

From the three main prospected localities in Sabah, a total of 254 species from most spiders families (for practical reasons the mygalomorphs and the salticids were excluded) could be distinguished. Of these, 35 species could be identified as described species, seven of which are clearly synanthropic.

On Mt Kinabalu (1500-1900m), 135 species were collected in 18 days (41 species represented by one specimen only); 25 species were collected in two collecting days at Poring Hot Springs, lower down on the mountain slope at 500-600m; four of these were shared with the 1500-1900m site (see Table 1). For six of the 19 described and named species this is the type locality (Deeleman-Reinhold, 1980, 1987; Levi, 1982). 132 species (85%) were collected only in Kinabalu; 24 species were also found elsewhere.

Oonopidae
Dysderina sp. (1)
Gamasomorpha sp. (2), Sabah
Ischnothyreus peltifer (Simon), world tropics
sp. (5)
Opopaea ? sp. (1), Sabah
Orchestina sp. (1)
Plectopilus sp. (1), Sabah
Xyphinus sp. (1)
Tetrablemmidae
Ablemma sp. (1)
Ochyroceratidae
Merizocera sp. (1)
Speocera sp. (1)
Pholcidae
Calapnita phasmoides Deeleman, Borneo
Smeringopus pallidus (Blackwall), world
tropics
Pholcus sp. (2) (1) in logged area
Spermophora sp. (1), Sabah
Belisana sp. (1)
Heteropodidae
Heteropoda sp. (1)
sp. (1), in logged area
Olios sp. (1)
Ctenidae
Ctenus sp. (1)
Gnaphosidae
Micythus sp. (1)widespread
Clubionidae s.l.
Clubioninae
Cheiracanthium sp. (1)
Clubiona sp. (3)
Castianeirinae
Aetius sp. (1)
Phrurolithinae
Sesieutes sp. (1), Sabah
Corinninae
Undescribed genus (1)
Palpimanidae
Boagrius sp. (1)
Zodariidae
Malinella sp. (2)
Thomisiidae
Borbonopactus sp. (1)
Loxobates sp. (1), in logged area
Pagida sp. (1), in logged area
Peritraeus sp. (1)
Synema sp. (1)
Talaus sp. (1), in logged area
Tmarus sp. (2), in logged area
Pisauridae
Polybaea sp. (1)
Oxyopidae
Oxyopes lineatipes C.L. Koch, widespread
sp. (1)
Tapponia superba Thorell, widespread
Lycosidae
Hippasa
Wadicosa birmanica (Thorell), widespread,
in logged area;
Pardosa pusiola (Thorell), widespread
Hahniidae
Alistra sp. (1)
Hersiliidae
Hersilia sp. (1)
Theridiidae
Achaearanea sp. (1)
Argyrodes sp. (1)
Cephalobares sp. (1)
Chrysso sp. (1)
Coleosoma sp. (1), Sabah
Coscinida sp. (1)
Dipoena sp. (2)
Episinus sp. (1)
Janula sp. (1), Sabah
Theridion sp. (4)
Undescribed genus (1)
Mimetidae
Mimetus sp. (1)
Mysmenidae
Undescribed genus (1)
Anapidae
Pseudanapis paroculus Simon, widespread
Leucauge sp. (1), Sabah
sp. (1)
Glenognatha sp. (1)
Araneidae
Caerostris sp. (1)
Cyclosa bifida Doleschall, widespread
mulmeinensis (Thorell), widespread
Gasteracantha sp. (1)
Gea subarmata Thorell, widespread
Larinia phthisica L. Koch, widespread
Milonia trifasciata Thorell, widespread
Neoscona nautica L. Koch, world tropics
sp. (1)
Poltys sp. (1)
Undescribed genus I (1)
Undescribed genus II (1)
Linyphiidae
Undescribed genus (1)
Uloboridae
Philoponella sp. (2)

Table 2. Spiders from Danum Valley Field Centre, primary lowland forest, 8 collecting days in May; some species, mostly Thomisidae, in freshly logged area. Family order is 'phylogenetic'. List gives no. of undescribed species in parentheses and notes on species.

Compared to the lowland catches, a predominance of Linyphiidae was found.

In primary lowland forests around Danum Valley Field Centre in East Sabah, 90 species were collected in 9 days (Table 2); 14 species have been previously described. Of these, 67 species (70%) were only found at Danum, and 23 were also found elsewhere. In a freshly logged area, thomisids were particularly diversified.

In the secondary forest of Signal Hill in the township of Kota Kinabalu, 16 species were collected, 7 of which could be identified to species. Eight species were found also elsewhere, and 8 species (50%) were collected only on that site.

DISCUSSION

The main conclusion is that in tropical forests, spider species known from only one locality are enormously preponderant even though all distribution types from cosmotropical to very restricted ranges were encountered.

In a total of 254 species from the three localities (Tables 1-3), 207 were collected at one locality only, 92 of which were 'singletons'. Is this due to the lack of data only, or is a high percentage of endemic species real? This phenomenon occurs much more frequently in some families than in others. Quite often, in adjacent localities a sister species is found. In a long-term inventory of a 1-2 km^2 area on the northern side of the Sibolangit range, on Gunung Leuser in Sumatra (Deeleman-Reinhold, unpublished data), spiders were collected once a week for two years. A similar study was conducted on the other side of the ridge. Less than half of the species were found on both sides of the range! Therefore, endemism in spiders seems characteristic of primary rainforests, even though the real extent of distribution ranges will only be revealed after long and extensive sampling. For example, recent studies on south-east Asian Linyphiidae (Millidge and Russell-Smith, 1992) report 27 species, 26 of which new, described in 11 new and four known genera; all new species were recorded from only one locality (see also Scharff, 1992).

Also, widely distributed species were often found in human-made habitats. In such habitats most species described in the last century were found. In the course of identifying large south-

Oonopidae	*Psilochorus* sp. (1)widespread	sp. (1)
Ischnothyreus peltifer (Simon), world tropics	**Ctenidae**	**Tetragnathidae**
sp. (1)	*Ctenus* sp. (1)	*Leucauge* sp. (1)
Plectoptilus sp. (1)	**Clubionidae** s.l.	**Araneidae**
Ochyroceratidae	*Oedignatha scrobiculata* Simon, widespread	*Neoscona punctigera* Doleschall, widespread
Psiloderces sp. (1)	**Palpimanidae**	**Uloboridae**
Theotima minutissima (Petrunkevitch), world tropics	*Boagrius* sp. (1)	*Uloborus humeralis* Hasselt, widespread
Pholcidae	**Theridiidae**	
Uthina luzonica Simon, widespread	*Janula* sp. (1)	
	Theridion tenuissima Thorell, widespread	

Table 3. Spiders from town-park Signal Hill, Kota Kinabalu (2 collecting days). Family order is 'phylogenetic'. List gives no. of undescribed species in parentheses and notes on species.

east Asian collections it appeared that the majority of the species described prior to the early 20th century occur in habitats created by humans rather than in the rainforests. Thus, the spider fauna of the latter is still almost unknown.

A high degree of endemism seems to occur in certain families; other families which include a relatively high number of widely distributed species are Araneidae, Gnaphosidae, Oonopidae, Pholcidae and Salticidae. Occasionally, one or two species in a family are able to disperse considerably, whereas their relatives have remained limited to a restricted area. Among the best dispersers are some of the smallest known litter-dwelling spiders, with a body length of less than 1mm, which independently seem to have developed methods to overcome the vicissitudes of ballooning, e.g. the tiny armoured anapid *Pseudanapis paroculus* Simon is distributed over much of tropical south-east Asia both in primary and secondary forests. The small ochyroceratid *Theotima minutissima* (Petrunkevitch) and the oonopid spider *Ischnothyreus peltifer* (Simon) are distributed over the palaeo- and neotropics, where they live side by side with local congeners. Also larger spiders have been found to be widely distributed in humid forest, such as some *Cyclosa*, *Argiope*, *Acusilas*, *Neoscona* and *Gasteracantha* species, but also the delicate, almost transparent pholcid *Calapnita vermiformis* Simon.

The number of small-range species in both primary and secondary evergreen forests seems to be enormously higher than we are used to in temperate climates. Very few wide-spread species seem to occur naturally on Mount Kinabalu; more were found in lowland forest.

It is premature to estimate the total number of species present. Richest in species probably is the family Salticidae. Also numerous in species are the Theridiidae, Oonopidae, Araneidae, Clubionidae s.l. and Tetragnathidae in that order (see also Wanless and Hillyard, 1984 for Gunung Mulu).

Some genera have been particularly speciose in primary forest. In *Ischnothyreus* I found 11 species in Sabah (10 undescribed); in *Theridion* 11; in *Dipoena* 8; and in *Clubiona* 8 (all undescribed).

One final remark on diversity. Among the strongly represented families, diversity in the following families appears to be higher than average: Pholcidae, Clubionidae *s. lat.*, Tetragnathidae, Araneidae, Linyphiidae.

This study indicates that, when replacing primary forest by secondary plantations, the loss of species diversity of spiders is enormous.

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A REVIEW OF FACTORS INFLUENCING THE DISTRIBUTION OF SPIDERS WITH SPECIAL REFERENCE TO BRITAIN

ERIC DUFFEY

Duffey, E. 1993 11 11:. A review of factors influencing the distribution of spiders with special reference to Britain. *Memoirs of the Queensland Museum* 33(2): 497-502. Brisbane. ISSN 0079-8835.

Available data on factors influencing spider distribution are synthesized using mainly British and other European information. The importance of landscape history is stressed, in fragmenting ancient natural habitats and creating new ones. It is postulated that this has reduced the number of specialists and allowed a range expansion of pioneer and euryoecious species. A tentative classification of life strategies is proposed. Habitat diversity and microspatial distribution are discussed with examples. □*Spiders, habitat preferences, geographic distribution, life strategies.*

Eric Duffey, Cergne House, Wadenhoe, Peterborough, PE8 5ST, United Kingdom; 3 November, 1992.

Many attempts have been made to categorise the habitats of spiders according to their preferences for dampness, dryness, shade, light, warm or cool temperatures. In addition, increasing knowledge derived from extensive collections made during the last 50 years in Britain and the rest of Europe have made it possible to draw distribution maps (Locket *et al.*, 1974; Ransy and Baert, 1985, 1987a, 1987b; Janssen and Baert, 1987; Ransy *et al.*, 1990; Alderweireldt and Maelfait, 1990; Canard, 1990), even though their incompleteness is acknowledged. The distribution of some species shows a clear influence of latitude and longitude, with north-south or east-west trends, or an association with major habitat formations. This paper discusses some factors which influence spider distribution, such as landscape history and geographic range, habitat preferences, adaptation to man-made biotopes and small-scale environmental differences, with the object of categorising the occurrence of species according to life strategy.

Islands of modest size such as Britain are poorer in species than adjacent continental areas. For example, the spider fauna of Belgium, a near neighbour, which is only 1/8th the size of Britain and has 75km of coastline compared with Britain's 19 000 km, and a lower landscape diversity, has almost as many recorded species (600) (Keckenbosch *et al.*, 1977) as Britain's 622 (Roberts, 1985-87).

Habitat labels based only on local information may be unsatisfactory, since (in Britain and the rest of Europe) we know that (a) some widespread species are found in different habitats according to where they occur in their geographic range; (b) within a restricted area some species are found only, or mainly, in 2 very different habitats, for example sand-dunes and marshes; (c) some species are so widespread that they are difficult to characterise in terms of habitat preferences; (d) species confined to only one specialised habitat are generally few in number and often rare. Examples are presented in this paper.

Nomenclature follows Roberts (1985-87) for spiders and Anon. (1964-80) for plants.

LANDSCAPE HISTORY AND PATTERN OF SPIDER DISTRIBUTION

Britain was largely forested before human settlement but forests are now much modified scattered remnants. This extensive environmental change will have favoured some species and disadvantaged others. For example, when the surviving rare species associated with major formations in Britain are listed (Table 1) most are recorded for coastal systems which–apart from the more limited mountain tops–are the least modified components of the present-day landscape. Species which are regarded as 'characteristic' of major habitat formations (Ratcliffe, 1977) (Table 2) may also be identified. The high numbers recorded for grassland, dry heaths and coasts probably reflect a great expansion of range by open-ground species after forest clearance.

The extent of habitat modification and disturbance is difficult to quantify because the type and intensity of change varies from place to place. In the case of wetlands, however, there is a common factor in that alteration to the water table has a greater impact on the fauna than other uses made

TABLE 1. Numbers of British spider species in the IUCN categories Endangered, Vulnerable and Rare, assigned to major habitats (compiled by P. Merrett in Bratton, 1991).

Coast- dune, shingle, saltmarsh, cliff	24
Dry lowland heaths	14
Fens-mesotrophic to eutrophic	12
Deciduous woodlands in lowlands	10
Caledonian (ancient) pine forest, Scotland	5
Grasslands-acidipholous to calcicolus	7
Wet heath/bog—oligotrophic	7
Open moorland, uplands and mountains	4

of these areas by man. In 1969 11 fens in East Anglia were surveyed by a group of arachnologists hand-collecting for a total of 10 hours per site. Each hourly collection was kept separate. The similarity between the faunas of the 11 fens in terms of abundance of each species present was assessed using Mountford's Index of Similarity (Mountford, 1962). Three groupings were derived, of which 2 were more similar than either was to the third group. The 8 fens in groups 1 and 2 had survived with little change to their water regimes at that time, while the third group had suffered falling water tables and hence vegetation changes (Duffey, 1974). The mean numbers of species for groups 1 and 2 were 53.2 and 50.0, respectively, and 34.6 species for group 3. Most of the rarer and more specialised fen species (*Marpissa radiata* (Grube, 1859); *Hygrolycosa rubrofasciata* (Ohlert, 1865); *Neon valentulus* Falconer, 1912; *Carorita paludosus* Duffey, 1971; *Centromerus incultus* Falconer, 1915; *Maso gallicus* Simon, 1894) were recorded in groups 1 and 2.

HABITAT VERSATILITY IN SPIDERS

The ability of many spiders to live successfully in a range of different environments has been little studied. The best known examples are pioneer species that are good aeronauts and the first to colonise newly created habitats. Meijer (1977) discusses this for Dutch polders, and Duffey (1978) for croplands and grasslands. Not all aeronauts behave in this way. *Erigone arctica* (White, 1852) and *E. longipalpis* (Sundevall, 1830) are often abundant on coastal driftlines and saltmarshes but are rare inland. The former is found on mountainsides in Sweden (the late A. Holm, pers. comm.) and both have been recorded on inland saline areas as well as in sewage works.

TABLE 2. Numbers of British spider species assessed as characteristic of various major habitats (compiled by P. Merrett in Ratcliffe, 1977)

Grasslands	74
Dry lowland heaths	63
Coastal formations	53
Deciduous woodlands	34
Fens	31
Wet heath/bog	21
Open moorland	17
Caledonian pine forest	14

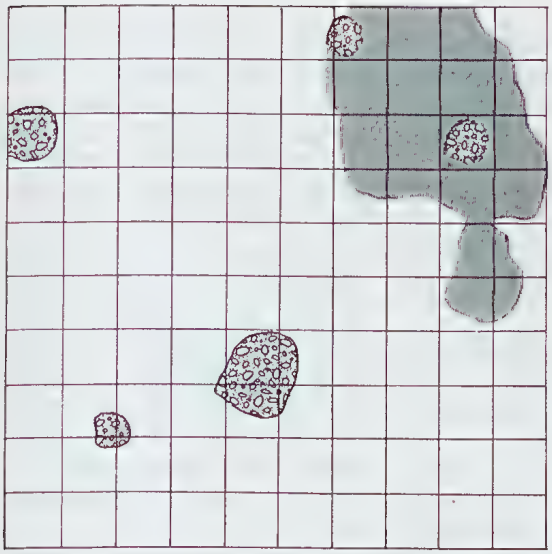
This provides evidence that they disperse over long distances but survive in only a few places.

Agricultural land has been colonised by species whose natural habitats are sand-dunes and stony open ground, for example *Troxochrus scabriculus* (Westring, 1851) and *Milleriana inerrans* (O.P.-Cambridge, 1884). *Porrhomma convexum* (Westring, 1861) is also frequent on cultivated land but elsewhere occurs in caves, mines, culverts (Locket and Millidge, 1953), and under stones by stream and lake shores (K. Thaler, pers. comm. and Duffey, unpublished).

The stone-filled filter beds of sewage works attract another cave species, *Lessertia dentichelis* (Simon, 1884), together with *Leptorhoptrum robustum* (Westring, 1851), whose natural habitat is freshwater marshes and wet meadows, and also *E. longipalpis* and *P. convexum*. The environment of filter-beds is completely artificial and uniform with stable temperature and high humidity, forming a 'super habitat' in which few species occur but in much higher numbers than found in nature.

The ability of some species to live successfully in two contrasting habitats was first noted by Bristowe (1939) and described as 'diplostenoecism' by Duffey (1974) and 'doppeltes ökologisches Vorkommen' by Schaefer and Tischler (1983). The best-known examples are those species found on coastal dunes and also in marshes–*Synageles venator* (Lucas, 1836), *Tibellus maritimus* (Menge, 1875), *Clubiona juvenis* Simon, 1878, *Hypomma bituberculatum* (Wider, 1834) and *Thanatus striatus* C.L. Koch, 1845. The last is also found in dry grasslands. *Sitticus rupicola* (C.L. Koch, 1837) is widespread on stony mountainsides in central Europe (Prószynski, 1978) but in England occurs only on coastal shingle banks.

Competitive relationships may also influence choice of habitat and hence distribution. *Zelotes electus* (C.L. Koch, 1834) is the characteristic species of this genus on coastal sand-dunes in



FIGS 1A-C. Distribution of spiders on 2.5x2.5m plot divided into 25x25cm quadrats on a Danish heathland.
1A. Vegetation map: Blank space, heather; lined shading, grass tussocks; cobbled, mosses, lichens and small stones.

	2	2	2	2					
3	4	2	6		2				1
5	4	3	6	2	3				
3	2	6	3	4	4	1	1	1	
1	3	5	7	3	3	4	2		
5	1	2	3	5	1	6	1	1	2
14	7	4	2	1	7	2	1	2	
2	5	3	3	3	7	1	3	3	
6	9	5	5	1	3	6	2	1	
3	2	7	2	2	4	7	2	5	

FIG. 1B. *Trichopterna cito*. A small web-spinning linyphiid almost confined to open ground with short, sparse vegetation; not a known active aeronaut nor a pioneer (Table 3) but a Narrow Specialist. Spread of heather eliminates it.

Britain whereas *Z. pusillus* (C.L. Koch, 1833) is associated with inland heaths, dry grasslands and open, stony ground. However, *Z. electus* was found (Anon., 1979) to extend only as far north as south-east Scotland and at higher latitudes was replaced on the coastal dunes by *Z. pusillus*.

All these species can adapt to different environmental conditions and emphasise the need to study habitat selection throughout the whole geographic range of a species before its distribution status can be understood.

EFFECTS OF HABITAT FRAGMENTATION

Several distribution maps in Locket *et al.* (1974) show widely scattered records for certain species which may indicate a decline from a former continuous distribution.

Lepthyphantes midas Simon, 1884 is an ancient forest specialist and is associated with loose bark and dead timber or birds' nests made of twigs. It is only known from 4 scattered sites in Britain where ancient forest survives. Similarly, wetlands have suffered serious losses, including the Fen Basin, East Anglia, which was progressively drained from Roman times and lost the remaining large areas of marsh in the mid-19th century. The local lycosid *Hygrolycosa rubrofasciata* (Ohlert, 1865) survives in the two remaining fenland areas and also in numerous small fen relicts around the

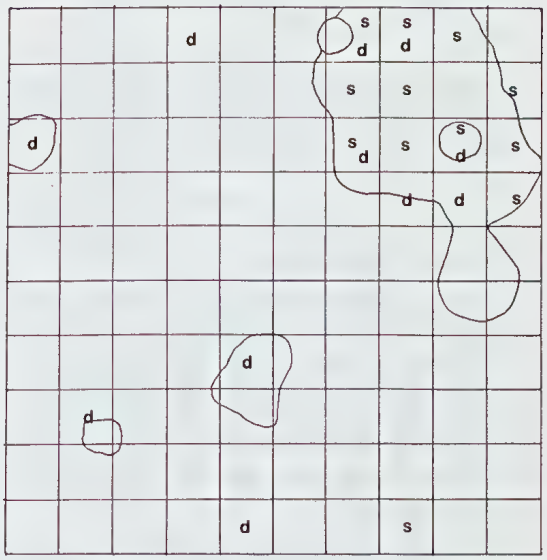


FIG. 1C. Other species preferred cover of heather plant or grass tussocks, e.g. *Scotina gracilipes* (Blackwall, 1859) (s) and *Dipoena prona* (Menge, 1868) (d). Each record refers to a catch of 1-5 individuals.

TABLE 3. Classification of life strategies and adaptability to environmental diversity based on British spiders.

PIONEER SPECIES
Active aeronauts which disperse freely, exploiting newly created open ground where competition is low. Widely distributed in temporary or changing habitats such as agricultural cropland, gardens, urban areas, leys and other types of disturbed ground or vegetation.
GENERALISTS
Common species with a capacity to adapt to a wide range of semi-natural habitats and permanent artefacts in the man-made environment. May be difficult to assign to a particular habitat.
BROAD SPECIALISTS
A. Widespread, euryoecious, or 'characteristic' species (Table 2) associated with major habitats such as deciduous woodland, marshes, heaths or ancient grassland, but may be found in many different variants of the chosen major formations.
B. Diplostenoecious species, mostly widespread and associated with 2 different habitats but usually more common in one than the other. Occasionally much more abundant in man- made habitats than in the natural environment. This grouping grades into species successful in 3 or more different environments.
NARROW SPECIALISTS
Stenoecious species which seem confined to clearly defined habitat. Includes rare species in low numbers and others which may be locally abundant, although confined to a restricted area because the habitat is scarce.

margins of the Fen Basin. Are these relicts of a former more extensive distribution?

Lowland heathland has also suffered severe losses, having been reduced to many small fragments by agricultural reclamation with a consequent loss of biodiversity (Webb, 1990). *Eresus niger* (Petagna, 1787) was formerly more widespread in heaths in southern England but is now known from only one locality where the population is small.

In contrast, some species are able to live in a range of different habitats, and thus overcome the problem of fragmentation. If this characteristic is also combined with active aeronautic dispersal, the chances of finding isolated suitable environments will be further enhanced. For example, *Pardosa palustris* (L., 1758) is the most active aeronaut of the common lycosids found in Britain and northern Europe (Richter, 1970). Few have been recorded in a wide variety of habitats, including marshes, grasslands, heathlands, and agricultural crops, but occasionally is found to be dominant, as in moist hay meadows in river valleys and on some sand-dunes. In a survey of dune systems in Scotland (Anon., 1979) it was the most abundant lycosid, although it was not recorded on all the dune areas which were studied. It seems that the active aeronautic behaviour of *P. palustris* enables it to move about freely and its ability to exploit many different habitats gives it a high ranking as an opportunist. Kessler (1973) also showed that *P. palustris* is able to produce more eggs per unit of body size under field conditions than 7 other *Pardosa* species. This may be an advantage when colonising new areas.

Adaptability to environmental diversity varies from species to species, so that a gradient exists from those which are very widespread (usually many species) to those which appear to be confined to a specialised habitat (relatively few species). The different components of this gradient are outlined in Table 3, and modified from Duffey (1975a).

HABITAT DIVERSITY AND MICROSPATIAL DISTRIBUTION

The structure of the vegetation, the litter layer and physical features of the environment have a strong influence on spider distribution and species composition (Duffey, 1962, 1968, 1974; Edwards *et al.*, 1975; Uetz, 1991). There is evidence that all species, however widespread, are influenced in some way by habitat structure. This was shown by comparing the fauna in different quadrats of a simple vegetation type on a Danish heathland (Duffey, 1974). Fig. 1 shows the differences in species and numbers of spiders between 100 25x25cm quadrats in a block measuring 250x250cm. The vegetation consisted of a heather plant (*Calluna vulgaris* (L.) Hull, 1808) in one corner of the block, and a few scattered grass tussocks of *Deschampsia flexuosa* ((L.) Trin., 1836), while most of the area was covered with mosses, lichens and small stones. The species in Fig. 1 occurred in clearly defined microhabitats. *Trichopterna cito* (O.P.-Cambridge, 1872), which was widespread in the open ground of moss and lichen, avoided the heather, and was also absent from 4 quadrats on the right-hand side of the sampling area which

had been trampled. Similar results are reported by Jocqué (1973), who studied the fauna of different types of woodland litter layers in Belgium. On a heathland ranging from dry to wet areas, Snazell (1982) sampled the spider fauna by pitfall trapping at 154 random points over 12 months. By Principal Components Analysis on the 45 most numerous species he was able to show a wide gradation from specialised to broad habitat preferences, which conform well with the categories in Table 2.

In an experiment in tall grassland in England, faunal changes were recorded in grass litter modified by trampling. Samples of grass litter enclosed in nylon-mesh bags (20x20x8cm) received 3 different treading treatments (5 treads/month, 10 treads/month and an undisturbed control series) (Duffey, 1975b). There were 25 replicates in each case. After 12 months the volume of the litter in the controls had fallen by 50 % due to natural decay, but those having had 10 treads/month had fallen by 81 %. Of the 10 most frequent species, 5 were eliminated by the treading after 12 months, and the total numbers of all species fell by 84 %. Of the 5 remaining species, 3 showed little response to the treading, their numbers falling only marginally. The higher level of treading in this experiment was very light compared with that on a public footpath in a popular area, but the effect on the litter fauna was quite dramatic.

CONCLUSIONS

The modification of the European landscape through many centuries has been the greatest influence determining the distribution of spider species. Natural and near-natural habitats are now rare, as are the specialist species associated with them. Today many species have adapted to man-made environments, whether permanent or temporary, and those preferring open-ground conditions have greatly expanded their range. A gradation of life strategies (or adaptability) from pioneer species to narrow specialists is proposed. Superimposed on these factors are the influences of major climatic zones and the microspatial variations in the abiotic environment. All these features should be considered when defining the distribution and habitat characteristics of a species, drawing on evidence from the whole geographic range.

ACKNOWLEDGEMENTS

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THE DEVELOPMENT OF THE ASYMMETRICAL WEB OF *NEPHILENGYS CRUENTATA* (FABRICIUS)

JANET EDMUNDS

Edmunds, J. 1993 11 11: The development of the asymmetrical web of *Nephilengys cruentata* (Fabricius). *Memoirs of the Queensland Museum* 33(2): 503-506. Brisbane. ISSN 0079-8835.

In the field, young *Nephilengys cruentata* (Fabricius) remain on the barrier threads of their mother's web for about ten days, before moulting. Some do not initially disperse far, and may even remain on the barrier threads to build their first web. These first webs are complete orbs. As the spiderlings grow the hub of the web is spun approximately three quarters of the way up the web; later there are no spirals above the hub. At this stage some spiders join the hub to the barrier, forming a 'tent' under which the spider rests. The true retreat, of a tube that is closed at the end away from the hub, develops gradually as the spiders grow further.□*Nephilengys, web development, evolution of webs.*

Janet Edmunds, Mill House, Mill Lane, Goosnargh, Preston PR3 2JX, United Kingdom; 12 November, 1992.

Nephilengys cruentata (Fabricius) is common throughout tropical Africa. In Ghana it lives in savanna and forest edge areas. Under natural conditions it attaches its web to trees, but it has frequently adapted to attaching it to dwellings. It was very common at Legon in such situations. The adult female is large but the male is much smaller. The webs of larger spiders are usually a roughly triangular partial orb. The hub is at the upper apex, where there is a cylindrical retreat, closed at the end away from the hub. There is an extensive barrier above and behind the viscid web; the main attachment between the two is at the hub. The hub and retreat are often in the angle between a wall and the ceiling or overhang. This paper presents data on the shape of the web of *N. cruentata* from the earliest instars to adults.

METHODS

Spiders of all ages were observed living on the verandahs of a private dwelling and of the Zoology Department at Legon, but it was not possible to follow individual spiders in the field or captivity. Web size and length of the first leg of each spider were measured, although the relation between spider size and instars was not determined. The vertical asymmetry, lateral asymmetry and shape (circularity) of the web were determined from the ratios of vertical radii, horizontal radii and the two diameters respectively, all measured to the nearest 5mm; N for all figs is given in Table 1.

RESULTS

The cocoon is laid close to the web, often on a wall or ceiling. When the spiderlings emerge, they remain close to where they have emerged in a tight bunch on the barrier web for about ten days, spinning extra irregular threads. After the first post emergence moult, they disperse, but many remain close to the mother's web, some even building their first catching web in the threads of the barrier web.

When the spiders are grouped into different size classes based on leg 1 length, the extent of the web below the hub increases with each succes-

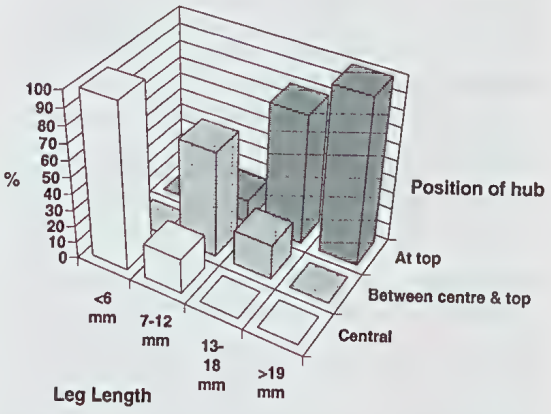

FIG. 1. Changes in vertical asymmetry in webs of *N. cruentata* with different leg lengths. At top: ratio of upper to lower radius = 0; Between centre and top: ratio of upper to lower radius >0 <1; Central: ratio of upper to lower radius = 1 .

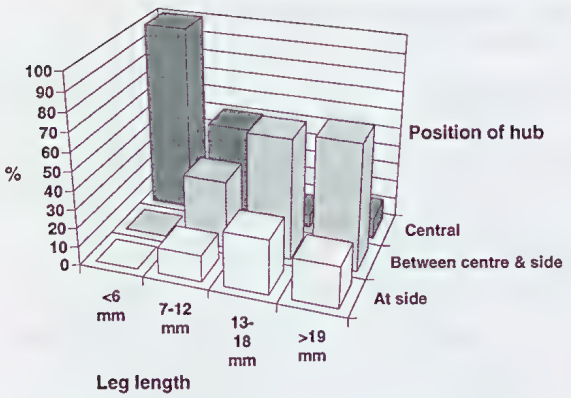

FIG. 2. Changes in lateral asymmetry in webs of *N. cruentata* with different leg lengths. At side: ratio of two horizontal radii = 0; Between centre and side: ratio of two horizontal radii >0 <1; Central: ratio of two horizontal radii = 1.

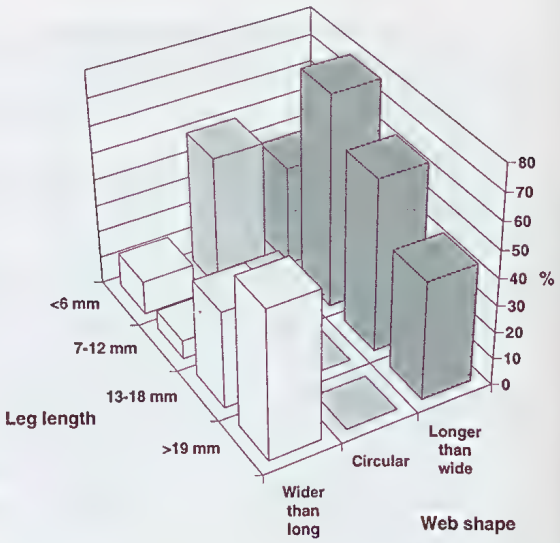

FIG. 3. Changes in shape in webs of *N. cruentata* with different leg lengths. Longer than wide: vertical diameter > horizontal diameter; Central: vertical diameter = horizontal diameter; Wider than long: vertical diameter < horizontal diameter.

sive class, while that above the hub increases slightly before decreasing to zero (Table 1).

The vertical asymmetry increases with size (Fig. 1): spiders with leg 1 <6mm spin complete orbs. As they grow, less web is spun above the hub, so that the hub is then about three quarters of the way up the web. Larger spiders, with leg 1 >19mm have no web above the hub. Because of the difficulty in following individual spiders, the time span over which these web changes occurred is not known.

Early webs are symmetrical laterally (Fig. 2), but webs of larger spiders show greater variation and may be markedly asymmetrical laterally; at the extreme the hub is completely to one side. Some early webs are also circular or nearly so (Fig. 3), however very few webs of spiders with leg 1 > 6mm have the vertical and horizontal diameters of the same size.

During these changes in the proportions of the viscid web, the barrier increases (Fig. 4). The very first webs have no barrier or just a few threads, which are attached to the orb at only a few points. But over some days more threads are added, until the barrier is a fairly dense cone shaped tangle behind the orb, and more firmly fixed to the web. Small pellets of detritus, similar in size and shape to the spiderling and of the same pale grey colour, usually occur in the barrier (Edmunds and Edmunds, 1986). These may deflect attacks of potential predators.

The development of the retreat increases with the size of the spider (Fig. 5). Spiders with the hub

TABLE 1. Body size and web dimensions (in mm) in different size classes (based on leg 1 length) of *Nephilengys cruentata*.

Leg 1 length	<6	7-12	12-18	>19
Body size	<3.5	3.5-7.0	7.0-9.0	>9.0
N	8	14	14	9
Hub-web top:mean	38.1	47.1	19.2	0
range	25-50	0-80	0-100	0
Hub-web bottom: mean	38.1	109.3	180.0	478.9
range	25-50	45-170	140-260	200-700
Web Width: mean	73.8	117.9	177.4	431.1
range	70-90	80-180	80-290	240-850

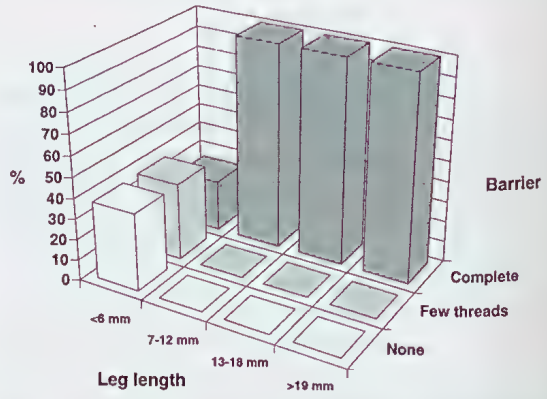

FIG. 4. Development of barrier in webs of *N. cruentata* with different leg lengths.

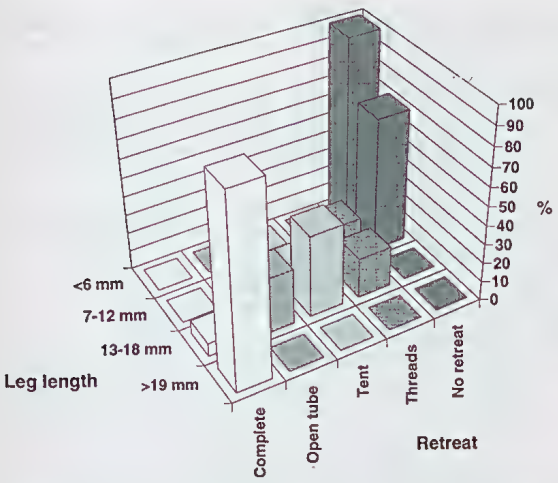

FIG. 5. Development of retreat in webs of *N. cruentata* with different leg lengths.

at the centre or part of the way up the web rest at the web hub and there is no retreat. When the hub is built at or very close to the apex, the first stages of a retreat are formed as a denser group of threads within the barrier close to the hub. As more threads are added, this becomes a roof-like tent between the hub and the barrier, or sometimes an open ended tube. Spiders with leg 1 >19mm normally had a closed tubular retreat, like an adult.

Early webs are very fine, and it is not easy to see the details of the individual threads. However, a complete web appears to be spun in one operation, unlike larger webs which are spun in two or more sections on different days. The temporary spiral does not appear to be left up, though more detailed observations would be needed to confirm this. Larger spiders leave the temporary spiral in the finished web.

DISCUSSION

The webs of most adult female Nephilinae are not typical orbs. Most *Nephila* species build incomplete orbs, with the hub near the top (Robinson and Robinson, 1973, figs 2, 20; pers. obs.). However, unlike *Nephilengys*, there are threads above the hub, including in some instances a few sticky spirals. In *Nephila plumipes* large, probably mature, females were seen in Brisbane, Australia, that had several sticky radii above the hub. However, in at least some individuals, these appeared to have been laid as pendulum turns, rather than complete spirals (pers. obs.). *Nephila* does not build a retreat and the spider rests at the hub. Like *Nephilengys*, there are barrier webs, though on both sides, and often above the orb. These are supportive and probably also defensive (Robinson and Robinson, 1973). *Herennia ornatissima* (Doleschall) constructs a very long web, with almost parallel sides (Robinson and Lubin, 1979). The spider sits in a cup-shaped depression of dense silk that forms the hub. It is towards the top of the web, though there are several sticky spirals above it. The spider has no barrier web, but as it builds very close to tree trunks, it would be difficult to find a place to build one.

Larger juvenile Nephilinae build webs like the adults, and a few observations have been published on the very early webs. The first webs of *Nephila clavipes* (Linnaeus) are circular (Comstock, 1948; Levi and Levi, 1968). Brown and Christenson (1983) give measurements of the webs of *N. clavipes* spiderlings between 2 and 9mm body length. The webs show an increase in vertical asymmetry as they grow. However, unlike *Nephilengys cruentata*, even the instars that spin the first catching webs had the hub approximately two thirds of the way up the web. Both species seem to spin the hub at the top of the web when they reach a similar size. Webs with spirals above the hub are spun by juvenile *Nephila maculata* (Fabricius) (Robinson and Robinson, 1973, figs 5, 6), and possibly by *Nephila senegalensis* (Walckenaer) (Clausen, 1987). The webs of juvenile *Herennia ornatissima* (Robinson and Lubin, 1979) are also more like a complete orb.

The fact that the earliest webs of at least some species of Nephilinae are complete orbs indicates that the orb is a primitive characteristic in them, and that the incomplete orbs of the larger spiders are derived. There are other spiders which have a highly modified orb-web, but build a more complete orb as a juvenile. Spiders of the genus *Scoloderus* build extremely elongated inverted ladder webs, with the hub towards the base. The juveniles of *Scoloderus tuberculifer* O.P.-Cambridge have webs that are far less distorted (Eberhard, 1975). However, even the smallest *S. cordata* (Taczanowski) have elongated ladders (Stowe, 1978). In *Araneus atrihastulus* from New Zealand, which builds a web that is elongated both above and below the hub, some of the proportions of juvenile webs are less extreme (Forster and Forster, 1985). It would be interesting to find the very early webs of other spiders with atypical webs, such as that of the spider that built the ladder web observed by Robinson and

Robinson (1972) in New Guinea, now identified as close to *Tylorida* (Eberhard, 1990b). Other aspects of web construction and use may be more derived in adults than in juveniles, such as the angle of the spring line and resting position of the spider in *Epeirotypus* sp. from Costa Rica (Eberhard, 1986). However, in the west African *Pararaneus cyrtoscapus* (Pocock), the conical horizontal webs of juveniles are more derived than the planar vertical of adult females (Edmunds, 1978).

If it is confirmed that young *Nephilengys cruentata* build webs in one piece and destroy temporary spirals, then the adult behaviour of leaving the temporary spirals in place is presumably also a secondary modification. There are other characteristics of the webs of Nephilinae that are derived. Despite their size, the webs of adults have a finer mesh compared to some other orb weavers (personal observation). Eberhard (1982, 1990a) concludes that some characteristics of the web building behaviour of *Nephila clavipes*, such as the unique method of laying the sticky spiral, are an adaptation to spinning a tightly meshed web, even though other aspects (e.g. frame construction) are primitive. Levi (1986), Eberhard (1990a) and Coddington (1990) classify the Nephilinae with the Metinae and tetragnathids, rather than with *Araneus* and its relatives. The derived nature of the partial orb of the larger Nephilinae would be consistent with this classification.

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DOES MIMICRY OF ANTS REDUCE PREDATION BY WASPS ON SALTICID SPIDERS?

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A common predator of spiders at Legon, Ghana, is the wasp *Pison xanthopus*, 96% of whose prey were salticids. The data from cells built by 31 wasps containing over 800 spiders are used to examine whether mimicry of ants gives protection against *Pison*. Comparison of salticids in wasp cells with those found on nearby vegetation shows that fewer ant mimics (*Myrmarachne* spp.) are taken than one would expect if wasps were capturing salticids in proportion to their occurrence, but also that some individual wasps specialize in capturing *Myrmarachne*. Implications for the searching image hypothesis are discussed. □*Batesian mimicry, ant-mimicry, Salticidae, predation, search image, Pison, Myrmarachne.*

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Ant mimicry has evolved in several spider families, e.g. Salticidae, Clubionidae, Thomisidae, Aphantochilidae and Theridiidae (Hingston, 1927; Mathew, 1954; Reiskind and Levi, 1967; Reiskind, 1977; Edmunds, 1974, 1978; Wanless, 1978; Oliveira and Sazima, 1984, 1985; Oliveira, 1988). Some of the most precise morphological and behavioural resemblances to ants occur in the salticid genus *Myrmarachne* which is widespread in both the Old and New Worlds, especially in the tropics (Wanless, 1978). At Legon, Ghana, three species of *Myrmarachne* are common, each one closely resembling one species of ant when it is full grown but a different ant species when it is immature (Edmunds, 1978). This mimicry could have two advantages for the spider:

1. It could deceive the ants and so enable the spider to creep up and prey on them. This is aggressive mimicry as may possibly occur in the thomisid *Amyciaea forticeps* (Mathew, 1954), and is well documented for the aphantochilid *Aphantochilus rogersi* (Oliveira and Sazima, 1984);

2. It could deceive a predator into mistaking it for an ant which that particular predator does not eat. This is batesian mimicry.

Myrmarachne do not normally attack ants, so there is no support for aggressive mimicry (Edmunds, 1978; Wanless, 1978). Indeed whenever an ant comes near they use their acute eyesight and quick reactions to avoid contact. This suggests a danger of being killed if caught by the ants (Edmunds, 1978; Wanless, 1978). Direct evidence supporting batesian mimicry is sparse. Edmunds (1974, 1978) argued that because few insectivorous birds prey on ants, the ant mimics associated with them would also escape predation. He further attempted to show that ant-mimicking spiders are less often taken by the wasp *Pison xanthopus* than are other salticids, but there were rather little data available at that time. More recently, the American ant mimic *Synageles occidentalis* was found being preyed on much less than are non-mimicking salticids by the philodromid *Tibellus oblongus*, and the large salticid *Phidippus clarus* ignored or avoided *Synageles* and ants in exactly the same way, while continuing to attack non-mimicking salticids (Cutler, 1991).

More data on the prey of *Pison xanthopus* are given here to test the theory that ant mimicry gives protection against spider-hunting wasps.

MATERIAL

Mud cells of *Pison xanthopus* were collected from window frames at the University of Ghana, Legon, Ghana between 1969 and 1973. Individual wasps build from 1-6 cells in a row. Each cell is stocked with 5-10 paralysed salticid spiders and an egg is laid on one of these. The spiders were preserved in alcohol and identified, usually to genus or species. They were also classed as either good ant mimics (*Myrmarachne*), poor ant mimics (*Cosmophasis* sp.) or non-mimics (other genera). Most of the spiders are now in the collection of the Natural History Museum, London. Identification of the spiders was confirmed by F.R. Wanless, and the wasp was determined by the late Professor O.W. Richards.

Spider	Habitat					In wasp cells
	Leaf litter	Short grass	Long grass	Shrubs	Tree trunks	
Good ant mimics						
Myrmarachne foenisex Simon				+	+	+
Myrmarachne elongata Szombathy			+	+		+
Myrmarachne legon Wanless				+		+
Myrmarachne uvira Wanless				+		
Poor ant mimics						
Cosmophasis sp.		+	+	+	+	+
Non-mimics						
Thyene sp.			+	+	+	+
Hyllus sp.			+			
Stenaeurillus sp.			+		+	
Rhene sp.					+	+
Cyllobelus rufopictus Simon	+					
Hasarius adansoni (Audouin)		+				
Schenkelia modesta Lessert					+	
Menemerus sp.					+	+
Pseudicius sp.					+	+
Other non-mimicking salticids		+	+			+

TABLE 1. Salticid spiders in five habitats at Legon, May-July 1973.

RATIONALE

If ant mimicry deceives wasps so that they do not capture ant-mimicking spiders as often as non-mimics, then the proportion of ant mimics to non-mimics should be lower in wasp cells than in the natural environment. If wasps are not deceived then the proportion of ant mimics should be the same. The test of this hypothesis is to compare the incidence of ant mimics in wasp cells with those found in the field.

WHERE DOES *PISON* HUNT?

First, the wasp's hunting range must be established so that a random sample of salticids can be collected from the same place. *Pison* is small, difficult to follow in flight, and was observed hunting on only a few occasions. Each time it was running and making short flights over leaves of shrubs. It was never observed on the ground or in grass, but as I spent more time examining shrubs than any other habitat, this is not conclusive. I therefore collected salticids from several different habitats at Legon. If the species of spider taken by wasps correspond with those found in one particular habitat then the wasps are probably hunting in that habitat.

The habitats are: leaf litter; short, regularly cut grass; long grass and herbage; 1-3m high shrubs; and tree trunks. The spectrum of spiders in wasp cells is most similar to those found in shrubs and trees (Table 1). The canopy was not sampled but probably has a similar fauna. However, it is unlikely that the wasps were hunting in short grass, leaf litter or long grass.

RESULTS

Spiders in Wasp Cells and on Shrubs

Some variation in the numbers of spiders caught by each wasp (Table 2) is due to the different numbers of cells completed by the wasps when collected. Cells with full grown larvae or pupae were ignored since the spiders in them were reduced to carapace cuticles, but cells with eggs or young larvae contained spiders that were intact and so are included. The spiders caught by each wasp came from 2-9 cells, e.g. on 3 Feb 1973, the first cell contained a pupa, the second a full grown larva, and the third had nine spiders but no egg. The wasp presumably was killed before fully provisioning this cell.

Of 872 spiders found, 837 were salticids (Table 2); 160 were 'good' ant mimics (i.e. *Myrmarachne* spp.), judged by the human eye, and a further 15 can be classed as poor (behavioural) ant mimics (i.e. *Cosmophasis* spp.). In 1973, every shrub in Zoology (twice) and in Botany (once) was searched (see Edmunds, 1978). All salticids found were scored as either a good mimic, a poor mimic or a non-mimic. The differences between types are highly significant ($\chi^2_{(2)} = 49.04$, $p < 0.001$; Fig. 1). *Pison* clearly take significantly fewer good ant mimics than they do poor mimics or non-mimics compared with their incidences in the environment.

However, wasps searching by running quickly over vegetation are unlikely to find spiders resting in their retreats beneath or between leaves. So perhaps the comparison should be made between the numbers of spiders in wasp cells and the numbers foraging on leaves (excluding those in retreats). These figures are also given in the upper part of Fig. 1 (the black bars only): 61.9% of spiders on shrubs were good mimics compared with 19.1% in wasp cells. This too is highly significant, again indicating that wasps take many fewer good mimics than poor or non-mimics ($\chi^2_{(2)} = 64.15$; $p < 0.001$). The proportion of poor

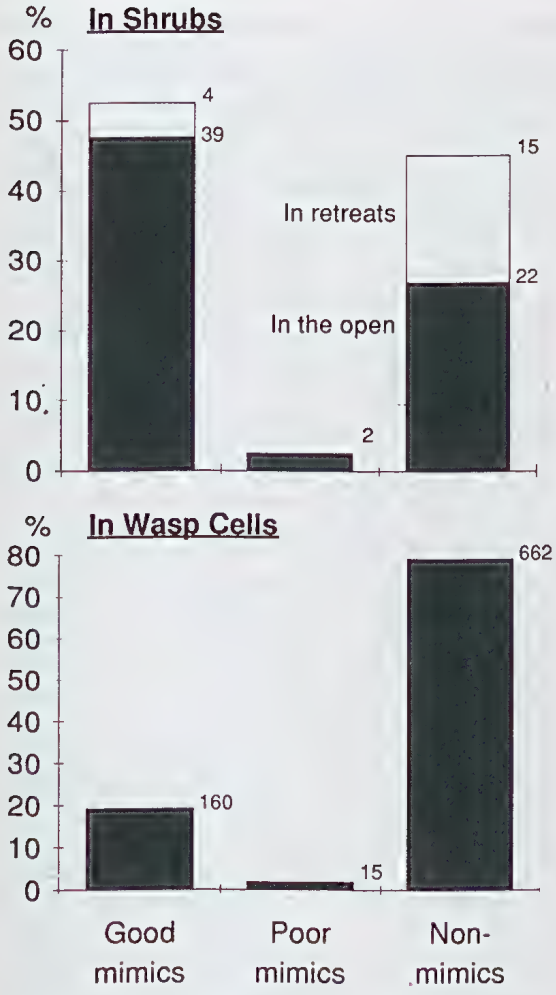

FIG. 1. Comparison of good, poor and non-ant mimicking salticids on shrubs and in cells of *Pison xanthopus*.

mimics taken by wasps is not significantly different from that of the non-mimics, so in the analysis that follows the poor (behavioural) mimic *Cosmophasis* is treated as a non-mimic.

Spatial or Seasonal Variation

These comparisons are of spiders on shrubs in February and May 1973 with spiders in wasp cells collected over 3.5 years. The relative numbers of *Myrmarachne* and of other salticids vary throughout the year and over different parts of the University campus, and this may account for the differences in proportions of spider prey taken by wasps. Evidence against this possibility is (1) that there was no significant difference in the relative numbers of *Myrmarachne* and of other salticids collected on shrubs in February and in May 1973 (Edmunds, 1978); (2) that the three wasp cells (taken 22 Jan- 3 Feb 1973) from close to where the shrubs were surveyed had between them eight *Myrmarachne* and 54 other salticids compared with 24 *Myrmarachne* and 26 other salticids on the shrubs on Feb 2; this difference is highly significant ($\chi^2_1 = 15.0$, $p < 0.001$); and (3) that the data (Table 2) show no clear evidence of spiders occurring at particular sites or in certain seasons. So, while there may be some variation in spider species at different times and places at Legon, such variation is unlikely to account for the very different numbers of salticids taken by wasps assuming that they take different species in proportion to their frequency in the population.

No Wasps Near Dangerous Ants

Most *Myrmarachne* taken by *Pison* were black and identified as *M. legon* and *M. elongata* (Wanless, 1978) but some immature specimens could not be identified. Only one specimen of the very common *M. foenisex*, in a total of 160 *Myrmarachne*, was taken. It was a juvenile whose body was red-brown and black (Edmunds, 1978, Fig. 1), quite unlike *Oecophylla*, but very similar to the smaller ant *Crematogaster castanea* which only lives close to *Oecophylla* (Edmunds, 1978). *M. foenisex* closely associates with the aggressive red weaver ant *Oecophylla longinoda*, of similar colour. Adult *M. foenisex* are probably too large for *Pison* to attack, but since it captures many young black *Myrmarachne* one might expect it to take young *M. foenisex* as well. Young *M. legon* are quite similar to young *M. foenisex*, but they do not associate with *Oecophylla* nor with *C. castanea*. Many young *M. legon* but very few *M. foenisex* were taken by *Pison*. Hence, *Pison* probably avoids hunting on plants overrun by *Oecophylla*.

If *Pison* does not hunt on plants with *Oecophylla*, then salticids found with these ants need to be omitted from the comparison of ant mimics and non-mimics on shrubs and in wasp cells (Table 3). Of salticids on shrubs, 49% are good ant mimics compared with 19% in wasp cells. This difference is highly significant, and remains so if spiders in retreats are excluded ($p < 0.001$).

Wasps clearly take fewer *Myrmarachne* than one would predict if they caught them in proportion to their occurrence in the environment. This is therefore good evidence for the defensive value of ant mimicry against predation by *Pison*.

		Mimics		Non-ant mimicking spiders											
Date	Place	My	Co	Ps	Rh	Te	Me	Vi	So	Th	Sa	Mo	Fi	Os	Of	All
28.9.69	Zool.				26											26
29.9.69	Zool.	2		8	1											11
13.1.71	Bot.	6		29	1											36
11.2.71	Bot.	34	1		1	6				2	2					46
12.3.71	Hill	4		44		1	1				1	2				53
11.4.71	Zool.	1		29										1		31
19.4.71	Maths			32			1							1		34
5.2.72	ISSER	15	11	2												28
15.2.72	Zool.			22					1				3			26
15.2.72	Zool.	10	2	4					2							18
18.3.72	Zool.														33[1]	33
27.3.72	Zool.	1		24	1											26
14.4.72	ISSER			36					1							37
16.5.72	Zool.			20	1											21
22.5.72	Zool.			28	1			1					1			31
22.5.72	ISSER			24					1							25
5.7.72	ISSER			28									2			30
6.7.72	ISSER	25														25
1.11.72	Hill	5		36		1		2					1			45
8.11.72	Zool.	15		16						1						32
13.11.72	Zool.	8		17	19									1		45
15.11.72	Zool.	18	1													19
18.1.73	Hill			26											1[2]	27
22.1.73	Bot.	6		25		1		8					2		1[3]	43
24.1.73	Bot.	1				9										10
3.2.73	Bot.	1		5			1			2						9
13.2.73	Agric						11									11
21.2.73	Hill	5		6												11
23.3.73	Hill	1		33		1	1									36
27.5.73	ISSER	2		25					1							28
28.5.73	Agric.			19												19
	Total	160	15	538	51	19	15	11	6	5	3	2	9	3	35	872

TABLE 2. Spiders in cells of *Pison xanthopus* at Legon, Ghana, 1969-1973. Key to Places at University of Ghana, Legon: Faculty of Agriculture, Agric.; Depart. of Botany, Bot.; Institute of Statistical, Social and Economic Research, ISSER; 36 Legon Hill, Hill; Depart. of Mathematics, Maths; Depart. of Zoology, Zool. [1] - 17 Thomisidae, 6 Theridiidae, 5 Clubionidae, 2 Oxyopidae, 1 Araneidae, 1 Selenopidae, 1 Philodromidae. [2] - Oxyopidae. [3] - Gnaphosidae. Taxon head is abbreviated in order: My, *Myrmarachne* sp.; Co, *Cosmophasis* sp.; Ps, *Pseudicius* sp.; Rh, *Rhene* sp.; Te, *Telamonia* sp.; Me, *Menemerus* sp.; Vi, *Viciria* sp.; So, *Sonoita lightfooti;* Th, *Thyene* sp.; Sa, *Saitis* sp.; Mo, *Mogrus* sp.; Fi, Fissident sp.; Os, other Salticidae; Of, other spider families.

Do Individual Wasps Hunt Specific Prey?

All wasps do not take a similar spectrum of spiders, but each individual preys on one or two species of spider (Table 2). Thus the first wasp in the table preyed on *Rhene* sp., the second and third on *Pseudicius* sp. and the fourth on black species of *Myrmarachne*. Ant mimicry was obviously of defensive value against the first three wasps who between them took only eight *Myrmarachne* out of 73 spiders (11%), while it failed to protect them from the fourth wasp which took 34 *Myrmarachne* out of 46 prey (74%). Overall, 25 individual wasps took only 38 *Myrmarachne* out of 693 spiders (5.5%), indicating that they had been deceived by the mimicry. The other seven wasps took 122 *Myrmarachne* out of 179 spiders (68.2%) indicating that they had overcome the defence of mimicry to the extent that they preyed almost exclusively on ant mimics (a wasp on 6 July 1972 took 25 *Myrmarachne* and no other spiders, while in the other six wasps *Myrmarachne* taken were never less than 45%).

For the poor ant mimic, *Cosmophasis*, the 15 spiders taken by wasps (Table 2) represent 1.7% of all salticids taken, or 2.1% excluding *Myrmarachne*. This is less than their relative frequency on shrubs (2.4% of all spiders or 5.1% excluding *Myrmarachne*), but the differences are not significant. However, one wasp (on 5.2.72) caught 11 *Cosmophasis* while all other wasps very rarely took them. Therefore, even poor mimicry of ants appears to give some protection against most wasps, but occasionally a wasp will specialize on this species, just as other wasps do with *Myrmarachne*.

Hunting by the Searching Image Method

The term searching image was used to describe the way in which tits (Paridae) collect caterpillars for their young: each bird tends to bring insects

TABLE 3. Percentages of *Myrmarachne* (Myrm) and other salticids on shrubs at Legon, and in cells of *Pison xanthopus*. Figures in brackets are numbers and percentages found in open (i.e. not in retreats).

Source of spiders	N	Myrm	Others	$\chi^2_{(1)}$
Shrubs-all data	82 (63)	52.4 (61.9)	47.6(38.1)	
Wasp cells	837	19.1	80.9	46.3 (59.8)
Shrubs-omitting *M. foenisex* & all spiders with ants *Oecophylla* & *Crematogaster castanea*	53(41)	49.1 (58.5)	50.9 (41.5)	
Wasp cells	836	19.0	81.0	25.5 (34.6)

of predominantly a single species for several days and then to abruptly switch to another species (Tinbergen, 1960). Tinbergen hypothesized that the birds recognised caterpillars by particular characters which they 'assimilated in a kind of learning process' and that in their search for prey they looked for these particular characters. Later authors have used the words 'searching image' and 'search image' interchangeably, but its definition has been refined following Croze (1970), Dawkins (1971), Krebs (1973), Lawrence and Allen (1983) and Guilford and Dawkins (1987). It is now generally understood to mean a perceptual change in a predator that temporarily increases its ability to detect particular cryptic prey which it has recently encountered. Searching image needs to be distinguised from various other types of preference that predators may show for particular prey (Krebs, 1973; Lawrence and Allen, 1983), so it is probable that the behaviour observed by Tinbergen which he called hunting by means of a 'specific searching image' would today not be considered a proven example of searching image behaviour.

Individual *Pison xanthopus* clearly concentrate on one or a few species of prey; is this because it hunts using a searching image or by some other method? In a recent critique of the search image concept Guilford and Dawkins (1987, 1988a,b) argue that all studies purporting to demonstrate searching images can actually be explained better in terms of variation in search rate. They make two predictions which can distinguish between the two hypotheses. First, the search rate hypothesis predicts that mimetic prey should take longer to find than non-mimics, so wasps that have learned to find them will slow down their search rate. The searching image hypothesis makes no such prediction. Second, the searching image hypothesis predicts that because of perceptual specialization, wasps concentrating on one type of prey will ignore others. The search rate hypothesis makes no prediction about concentration on one prey interfering with finding other prey. These observations do not explicitly test either prediction, but I consider that *Pison* is not hunting by adjusting its search rate because different wasps concentrate on different prey implying that capture of several prey of one species interferes with capture of other species. The two wasps at ISSER on 5th and 6th of July 1972 took very different prey. If they had been hunting simply with different search rates then the first wasp should have taken some *Myrmarachne* while the second should have taken some *Pseudicius*. This total concentration on one species of prey is not easy to explain on the search rate hypothesis.

If *Pison* is not capturing prey by adjusting its search rate, there are at least three other hunting methods that might result in the concentration on particular species of prey shown in Table 2:-

1. Wasps might have some sort of preference for one prey rather than another. This is unlikely if the preference is based on taste because the wasps sting but do not eat the prey.

2. Wasps could be searching in different places:-

a. Individual wasps might search in different microhabitats. If each species of spider lives in a slightly different microhabitat on the shrubs then individual wasps could catch different species of spider. Evidence in favour of this is the wasp on 18 Mar 1972 which concentrated on thomisid and other non-salticid spiders. Because it initially caught some of these spiders it is reasonable to suppose that it learned to hunt in particular areas or in a particular way such that it continued to catch these spiders instead of salticids.

b. Wasps might search in one area before going on to another. If spiders are clumped instead of being randomly spaced, then individual wasps hunting in the same general area could capture different species of spider. I often found two or three spiders of one species on a shrub so the distribution is clumped rather than random. However, there is no exclusion of one species by another, and the clumping may simply be of recently mated pairs or of parents with young that have failed to disperse. This impression has not been quantified, but I consider it unlikely that it could explain the extreme specialization on one species (Table 2).

3. The wasps may have a perceptual searching image as implied by Croze (1970). Wasps of other genera can learn the configuration of landmarks near their burrows (see Tinbergen,

1958), and this presumably involves some perceptual memory not unlike that in ourselves when we search for something with a particular image in our mind.

It is unclear which of the above methods of prey capture or if another method (e.g., Krebs, 1973) is involved. But certainly some such behaviour occurs both in *Pison* and in other wasps, e.g. the sphecid *Chalybion fuscipenne* (J. Edmunds, 1990).

CONCLUSIONS

Clearly, ant-mimicking spiders are common, more so than non-mimics in some habitats. Ant mimicry may give protection against wasps such as *Sceliphron* which prey on spiders of various families (Edmunds, 1974; J. Edmunds, 1990). The results confirm the suggestion from a preliminary, less rigorous study (Edmunds, 1974), that ant mimicry is of protective value against the specialist predator *Pison xanthopus*. The evidence that behavioural ant mimicry protects *Cosmophasis* against *Pison* is not conclusive; it may be protective against other wasps or against birds. Wanless (1978) and Curtis (1988) have evidence that spiders of this genus prey on ants, so this mimicry could also be aggressive rather than defensive in function.

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ABUNDANCE AND STRUCTURE OF FOSSORIAL SPIDER POPULATIONS

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Preliminary findings from an ecological study of large fossorial spiders, especially mygalomorphs, made in two locations in eastern New South Wales are given. The abundance of burrowing spiders was assessed in eight habitats: dry sclerophyll forests on sandstone and shale substrata, wet sclerophyll forests on sandstone, pastures, suburban gardens, pine windbreaks along roadside verges, coastal cliffs, and coastal swamps. The spiders included several species of Lycosidae, two Idiopidae and one Hexathelidae. Each species was restricted in its range of habitats and dominated the burrowing spider assemblage in only one or two habitats. The population structure of burrow sizes is described and compared for dense populations.□*Araneae, Idiopidae, Hexathelidae, Lycosidae, ecology, burrowing, sampling, distributions, habitats, size frequencies.*

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The field ecology of burrowing spiders in Australia has rarely used quantitative methods (but see Humphreys, 1988). Nor were field experimental manipulations used to test specific hypotheses, as in other branches of ecology (Underwood, 1990). These first quantitative observations of the abundance, size structure and habitat associations of large burrowing spiders from two locations near Sydney are part of environmental studies of funnelweb and trapdoor spiders.

The abundance, distribution and ecological interactions of fossorial spiders have been studied overseas in detail (see e.g. Buchli, 1969; Laing, 1978; McQueen, 1983; Conley, 1985; Fernandez-Montraveta *et al.*, 1991; Miller & Miller, 1991). The general biology, systematics and evolution of Australian mygalomorph spiders have been studied (see Main, 1976; Raven, 1988). The few quantitative ecological studies from Australia focussed on arid habitats (e.g. Main, 1987; Kotzman, 1990), upland sites (e.g. Humphreys, 1976), or used pitfall trapping (e.g. Curry *et al.*, 1985). In contrast, this study was on the warm temperate coast of eastern Australia.

METHODS

Study Sites and Habitat Types

Two locations near Sydney, New South Wales, and situated on Hawkesbury sandstone substratum, were sampled. Galston (33°41'S, 150°21'E) is a semi-rural village that has become suburban since 1972 and retains pockets of bush. Study habitats were located at 170-210m altitude. Patonga (33°30'S, 151°15'E) is a coastal village on the Hawkesbury River estuary and surrounded by Brisbane Waters National Park (Benson & Fallding, 1981). Study habitats were located at 5-80m altitude. At each location, all sites were within 2km of each other. I sampled six habitats in each location, although only three were present in both locations (Table 1).

Sampling and Analysis of Data

The sampling, October 1991-March 1992, was non-destructive. Quadrats (0.25 m^2) were randomly placed and then searched for individual spiders, burrows and trapdoors. All rocks, logs and litter in each quadrat were overturned and searched. I counted spiders, burrows or webs of each species in each quadrat. I sampled 10 quadrats in each of two sites in each habitat at each location (n=240 quadrats in all). The paired sites were replicate patches of habitat at the same elevation, as similar as possible, at least 100m apart and 100-1000m^2 in area. Site boundaries were located randomly on habitat maps before sampling. Spatial variability in each habitat was assessed by comparing spider densities in each pair of sites.

This design allowed a three-factor hierarchical ANOVA to examine the partitioning of spider abundance (as density=no. per quadrat) among the fully nested factors of Location, Habitat within Locations and Site within Habitat (Sokal and Rohlf, 1981). ANOVAs were done after assumptions were checked using Cochran's test for heterogeneity of variances. Means and standard errors of spider densities were calculated for each habitat and site. All statistical and graphical analyses were performed with SYSTAT Version 5 software (Wilkinson, 1990).

Location	Habitat type	Trees	Shrubs	Ground layer	Litter	Common spider	Less common spiders
Galston	Wet sclerophyl forest (WSF)	dense	dense	dense, rocks	dense, moist	*Atrax*	wolf
	Dry sclerophyll forest (DSF)	sparse	dense	little, rocks	dense, dry	none	*M. rapax*, wolf
	Garden lawns (GL)	none	few	grass	none	none	*M. rapax*, wolf
	Shale turpentine forest (STF)	dense	few	grass, logs	sparse, moist	*Atrax*	wolf, *M. rapax*
	Pine road verge (PRV)	pines	few	some grass	deep, dry	*M. gracilis*	wolf *M. rapax*
	Pasture	none	none	grass	little	none	none
Patonga	Wet sclerophyll forest (WSF)	dense	dense	dense, rocks	dense, moist	none	wolf, *M. rapax*, *Atrax*
	Dry sclerophyll forest (DSF)	sparse	sparse	little, rocks	dense, dry	none	wolf
	Sea cliffs (SC)	few	few	some roots, rocks	sparse, moist	*M. gracilis*	wolf, *M. rapax*
	She-oak swamp (SS)	sparse	none	some	dense, moist	*M. rapax*	none
	Garden lawns (GL)	none	few	grass	little	none	*M. rapax*, wolf
	Sports ground	none	none	grass	none	none	none

KEY TO HABITATS

DSF: characteristic open woodland (Benson & Fallding 1981; Benson & Howell 1990) in exposed positions on Hawkesbury sandstone plateaux, dominated by *Angophora costata*, *Eucalyptus haemastoma*, *E. gummifera* and *E. sparsiflora*; understorey of sclerophyllous shrubs of Fabaceae, Proteaceae and Myrtaceae; litter layer dense but dry; sandy soil; many ant nests and sandstone outcrops.

WSF: in moist gullies and other sheltered locations; many of the same tree species in the canopy, also *E. piperita* and *E. eximia*; compared with DSF; shrubs and creepers more mesophyllic and denser, with pockets of smaller trees–*Pittosporum undulatum*, *Tristaniopsis laurina* and *Ceratopetalum apetalum*; litter layer dense, moist, compacted; ant nests fewer; soil with more humus but about the same amount of rocky outcrops.

GL: cultivated exotic grasses regularly mown to <4 cm high, and probably also treated with fertilisers, herbicides and pesticides; little bare ground and almost no litter.

PRV: pine trees (*Pinus radiata*) along road verges, rarely mown and graded; deep litter of pine needles; soil with humus-rich, dry layer above hard clay-loam; understorey some *Acacia* and *Pittosporum* shrubs, & grasses.

STF: open forest in Fagan Park on ridgetop Wianamatta shale (Benson & Howell 1990), dominated by turpentine, *Syncarpia glomulifera*; other trees included *E. punctata*, *E. paniculata*, *E. acmenioides*, *E. resinifera*, *E. globoidea* and *A. floribunda*; shrub layer mainly of young trees; ground cover of grasses, logs and sparse litter.

SS: estuarine swamp dominated by she-oaks, *Casuarina glauca*; ground layer of *Juncus kraussi*, she-oak needles and saltmarsh succulents; lowest areas inundated by highest tides, but areas around sandstone outcrops higher and drier. Bushfire burnt this habitat and dry sclerophyll forest early 1991.

SC: sea cliffs immediately above rock platforms in the estuary; vertical walls of loamy soil covered with sparse leaf litter, mosses; some creepers and grasses common around roots of trees and shrubs on cliff edge. The least extensive habitat in area; 10 m or less high along seashore.

At Galston, the last habitat was pasture grazed by horse and cattle. Grass height, 6-40 cm; grasses probably fertilised infrequently; patches of bare soil rare.

At Patonga, a lawn and bare ground area around a sporting ground was the last habitat, very similar to the pasture at Galston except grass mown regularly to <4 cm high.

TABLE 1. Habitat characteristics, with spiders and occurrence of rocks, logs or tree roots. Common spiders = density > 1 per m^2. Abbreviations used in text are also given for each habitat.

Species were identified by burrow characteristics and observations of spiders seen at the burrow entrances either at night or during late afternoons on overcast days. Initially, I excavated at least 30 burrows of each type to obtain specimens for more thorough identification, and to investigate burrow structures and food remains. I measured maximum diameter of all burrows in quadrats (and outside them at some sites to increase sample sizes to >30). I tested for differences among size frequency distributions of burrow diameters using Kolmogorov-Smirnov (KS) 2-sample tests.

Sampling was repeated in late summer (Feb.-March) in some habitats to assess temporal variation between, before, and after the breeding season (roughly mid-sampling). In particular, abandoned burrows (with signs of decay and unoccupied) were noted. Burrows under rocks and logs were counted in some habitats because funnelwebs seemed restricted to such locations (e.g. short burrows in unconsolidated soils).

RESULTS

Spider Species

Six species in three families are here grouped into four ecological types. *Misgolas gracilis*

(Rainbow & Pulleine, 1918) is a large idiopid that builds deep, oblique burrows with a trapdoor among leaf litter in friable soils. The lids varied from flimsy and merely silk-covered with a thin layer of dirt to quite robust plugs for older spiders; this may be related also to the amount of litter present. In moist areas, the lid often grew moss and liverworts. *M. gracilis* was found only in SC and PRV habitats (Table 1).

Misgolas rapax Karsch, 1878 is also large with a burrow like *M. gracilis* but without a trapdoor. Often litter and vegetation around the burrow entrance were incorporated into the flared opening. Their burrows were more vertical than those of *M. gracilis*. The idiopids were identified using Main (1985), Mascord (1970, 1980). *M. rapax* was found in eight habitats but abundantly only in SS (Table 1).

Atrax robustus Cambridge, 1877 is the Sydney funnelweb spider (Hexathelidae). Several similar species are known from areas near the study locations, but all spiders collected were identified as *A. robustus* using Gray (1988), Scott (1980), Main (1985), Mascord (1970, 1980) (some smaller spiders were minimally confamilial). Most spiders were found under rocks and logs where characteristic silk tubes led to shallow burrows made in mostly unconsolidated soils and humus. Thus, all spiders were examined in the field but collections were limited to avoid depletion of the populations and for safety. *Atrax* was found in only two habitats but was a dominant in both (Table 1).

Wolf spiders (Lycosidae) built narrow, vertical burrows without lids and with much flimsier silk linings than did *M. rapax*. They were identified using McKay (1985) and references therein. The species excavated were *Lycosa godeffroyi* L. Koch, 1865, *L. leuckartii* (Thorell, 1870) and *Pardosa serrata* (L. Koch, 1877), the latter with characteristic palisades around the burrow. Other species but not excavated include *L. furcillata* L. Koch, 1867, *L. pictiventris* L. Koch, 1877, and *L. palabunda* L. Koch, 1877. Due to this uncertainty over the exact identity of the occupants of some burrows, I lumped data on all lycosid burrows into 'wolf spiders'. I found these in nine habitats but most commonly in WSF (at Patonga only) and PRV (Table 1).

Abundances

No spiders or burrows were found in quadrats sampled in the pastures or sports ground (Table 1, Fig. 1), although lycosids had been seen there. Neither habitat will be discussed further. Very

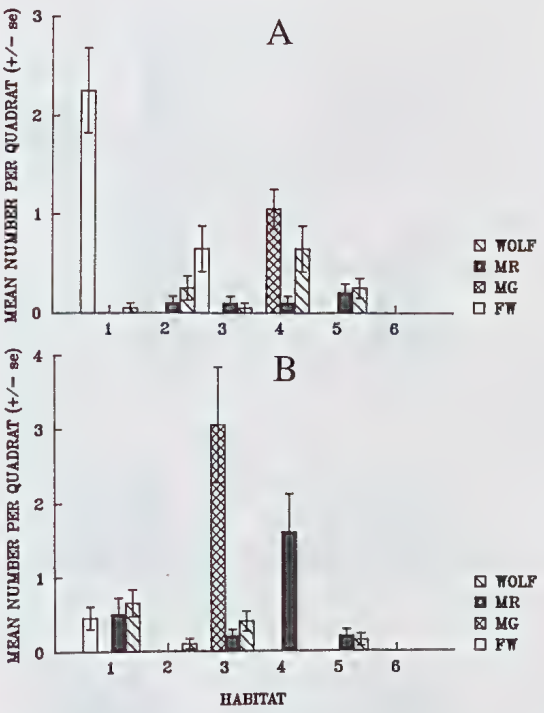

FIG. 1. Abundance (no. per 0.25m^2) of each species group versus habitat. A. at Galston, habitats are: 1=WSF, 2=DSF, 3=STF, 4=PRV, 5=GL, 6=pasture; B. at Patonga, habitats are: 1=WSF, 2=DSF, 3=SC, 4=SS, 5=GL, 6=sport ground. MR=*M. rapax*, MG=*M. gracilis*, FW= *Atrax* and WOLF=lycosids. Means and standard errors calculated from n = 20 quadrats in each habitat (i.e. sites were pooled).

sparse populations (of only lycosids and *M. rapax*) were found in open habitats–DSF and GL.

The abundance in the five occupied habitats at each location showed differences between habitats and species groups. An ANOVA of total spider density among locations/habitats/ sites (Table 2) showed no significant difference between the locations but large differences among the habitats within locations. At Galston, highest spider densities were found in PRV and WSF habitats, fewer in STF and very few in GL and DSF habitats. At Patonga, SC had the greatest densities, followed by WSF and SS habitats, and very few in the GL and DSF habitats.

Habitats with dense spider populations in either location were dominated by a particular species. At Galston, *Atrax* was the most common spider in the WSF and STF habitats but was not found in other habitats. At Patonga, *Atrax* was found only in the WSF habitat. *M. rapax* occurred in four habitats at Patonga and Galston, but

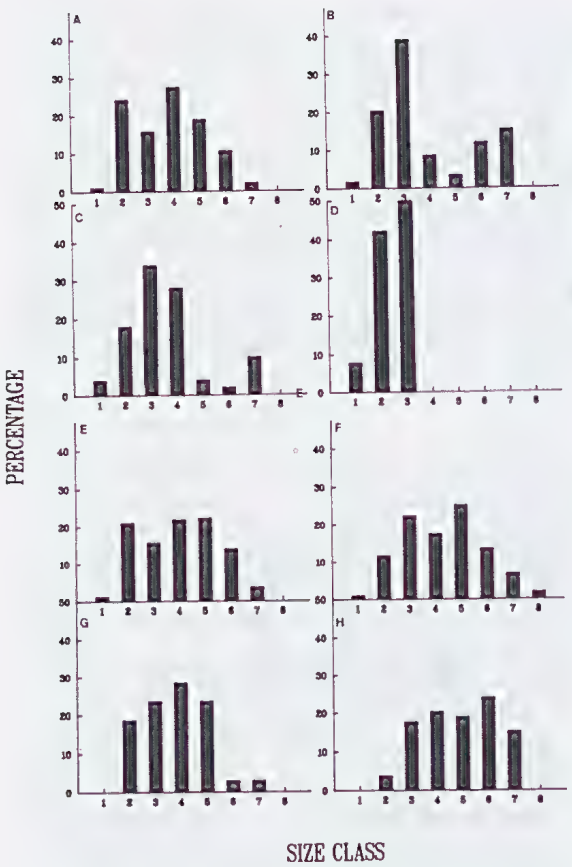

FIG. 2. Representative size frequency distributions of burrow diameter for dense populations of each species. Diameters grouped into eight equal size classes (to show large range with reasonable numbers in each): 1 =0-4.9mm; 2 =5-9.9; 3 =10-14.9; 4 =15-19.9; 5 = 20-24.9; 6 = 25-29.9; 7 = 30-34.9; and 8 ⩾ 35mm across the burrow entrance. A) *Atrax* from WSF, Galston, $n = 95$; B) *Atrax* from STF, Galston, $n = 59$; C) *Atrax* from WSF, Patonga, $n = 50$; D) lycosids from PRV, Galston, $n = 38$; E) *M. gracilis* from SC, Patonga, $n = 189$; F) *M. gracilis* from PRV, Galston, $n = 83$; G) *M. rapax* from SS, Patonga, $n = 102$; H) *M. rapax* from GL, Galston, $n = 79$.

dominated only in the SS habitat. *M. gracilis*, in contrast, was found in only one habitat in each location, but dominated the spider assemblage in both. In the SC habitat at Patonga, this species had the greatest mean density found in this sampling (>12 m^{-2}). Lycosids were found in five habitats at Galston and four at Patonga but they were never dominant. No species group was either positively or negatively correlated with any other in these samples (for all r, $P > 0.05$, $n = 200$).

The patchiness of mean spider abundance in any habitat was examined by the Sites within Habitat factor in the nested ANOVA (see Sokal and Rohlf, 1981). For total spider density and *M. rapax* alone, the two sites sampled within each habitat differed significantly (Table 2) . Because the sites were chosen randomly from the total habitat, this result indicates medium-scale variability in abundance of total spiders and *M. rapax* (i.e. at scales of about 100m).

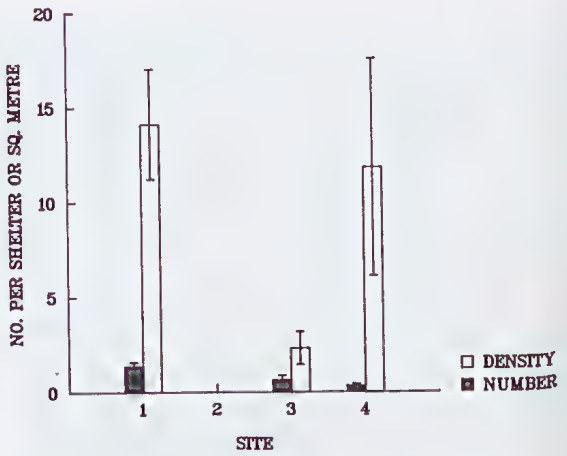

FIG. 3. Abundance of *Atrax* under rocks and logs in some habitats, expressed as no. per rock or log, and density (no. per m^2 of rock or log microhabitat). Area of each rock and log estimated from product of two, perpendicular linear dimensions in contact with the ground. Sites (sample sizes) were: 1=WSF at Galston (n = 43 rocks); 2=DSF at Galston (n=27 rocks); 3=STF at Galston (n =20 logs); and 4=WSF at Patonga (n=18 rocks).

Size Frequencies

Sample sizes of burrow diameter of sufficient number could be obtained only in habitats with dense populations. The burrow size structure (Fig. 2) of these populations showed differences (by KS tests) among species that were consistent across habitats. Very small burrows (< 5mm) were not found for *M. rapax* and only commonly for lycosids. *Atrax* showed bimodality in two habitats with the modes occurring at sizes corresponding to pre-reproductive juveniles and mature females (Fairweather, unpublished data). The other species had more unimodal burrow diameter frequency distributions. Lycosid burrows were much narrower on average than the mygalomorphs (Fig. 2). *M. gracilis* had the largest burrows overall.

Temporal Variation

Sampling before and after the breeding season showed few changes. The proportion of burrows of *M. gracilis* in the PRV habitat (Galston) that

were abandoned and decaying increased from 4.6% (n= 64) in December to 9.6% (n = 60) in March. These abandoned burrows did not, however, differ in size from the occupied ones (P> 0.05 by KS tests), suggesting no size selectivity in either mortality or abandonment by breeding males. The proportion of *Atrax* that were juvenile (i.e. <15mm and with no enlarged pedipalps on males) increased from November to February from 12% (n = 67) to 44% (n = 84) across all three occupied habitats.

Microhabitats

Within each habitat, burrows were found more frequently in particular situations. For example, *M. rapax* in the SS habitat (Patonga) were only found in areas around rock outcrops and none in the lower, inundated part of the swamp. *M. gracilis* was most abundant in moist, mossy patches in SC habitat (Patonga) and in areas covered with litter rather than bare ground in the PRV habitat (Galston). All *Atrax* webs encountered were seen under or against either rocks or logs, although thorough searches were also made amongst litter and in grass clumps. This prompted sampling centred on rocks or logs in three habitats at Galston and one at Patonga (Fig. 3). The abundance of *Atrax* under rocks and logs differed with habitats. None were found in DSF, despite abundant rocks. Counts of webs per rock or log were similar in the three occupied habitats. When expressed on a per area basis (i.e. m^2 of rock or log), the densities were much greater and differed among these habitats (Fig. 3).

DISCUSSION

This study suggests several hypotheses.

1. These species rarely encounter each other in nature, suggesting little competition occurs among them. I located each species group in more than one habitat, but they tended to dominate different ones. *Atrax* were favoured by apparently more moist conditions under shelter; although exfoliated rocks were abundant in the drier DSF habitat, no *Atrax* were found beneath them. *M. gracilis* was found in relatively exposed positions (sea cliff and road verge) with the most compact soil, whereas *M. rapax* dominated more open habitats (in terms of the litter and ground layers). Lycosids were the most widespread group, which may reflect that data of several species were lumped. Characterisation of habitats regarding soil, litter and vegetation conditions is needed.

2. Specific habitat characteristics favour different species. As well as the above habitat segregation, microhabitat preferences were also shown by several groups, most strikingly for *Atrax*, which was found in moist areas under shelter. Predictive relationships of abundance with environmental variables (e.g. soil nutrients, organic matter, compaction and moisture; litter amount, moisture and temperature; size and depth of shelter) may be established. Experiments on the effects of shelter, litter and moisture conditions on the abundance of these spiders are needed.

Factor	df	*F*-ratios				
		All spiders	*Atrax*	*M. gracilis*	*M. rapax*	Wolf
Location	1	0.19	1.21	0.38	1.93	0.003
Habitat	8	3.34*	73.43*	8.93	0.88	13.6*
Site	10	33.25	0.25	1.88	9.54*	0.31

TABLE 2. Three-factor, hierarchical ANOVA of density (number per quadrat) of total spiders and each species group analysed separately. * =Significance at P <0.05 level; df, degrees of freedom; df for residual, 180, and for total, 199. Total N=200 0.25 m2 quadrats; only five habitats used here.

3. Fossorial spiders respond adversely to many human impacts on their environments. This has implications for the interaction of these spiders with people and their activities. Few or no fossorial spiders were resident in habitats that lacked a litter layer or were regularly mown, watered, treated with chemicals or graded. The spiders can burrow in such open habitats (Fairweather pers. obs.), so perhaps the conditions may not be attractive to prey. There is some longer term evidence of declines in two of these populations associated with increasing urbanisation, direct disturbance, bushfire and vegetative change (Fairweather unpub. data).

4. Dense populations have been established for several years, at least. Size frequency distributions of burrows revealed juveniles in each dense population, therefore recruitment had occurred and no population was relict. Several very large burrows were present in the populations of the three mygalomorphs, probably indicating matriarchs (*sensu* Main, 1987). The abundance and size structure did not alter from October to March, which implies short-term stability for these long-lived spiders. Behaviour consistent with breeding behaviour over summer was seen for the mygalomorphs. Lycosids with egg sacs were seen only in spring and autumn.

5. Predation by some populations may strongly influence the assemblages of their prey. M. gracilis and *Atrax* were quite dense in particular

microhabitats, with some very large spiders; this and their predatory habits suggest that their role as predators in the ground-layer ecosystem would be worth further study.

In conclusion, large fossorial spiders are not evenly distributed across a variety of habitats, and each habitat is dominated in numerical terms by one or few species. Although the study was done in two contrasting locations, the generality of these results awaits scrutiny with further data as does the cause of any of the patterns described for the first time here.

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BIOGEOGRAPHIC PATTERN OF PHYLOGENY IN A CLADE OF ENDEMIC HAWAIIAN SPIDERS (ARANEAE, TETRAGNATHIDAE)

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The biota of the Hawaiian archipelago offers an ideal system with which to study the dynamics behind the evolutionary process, both because the islands harbour many speciose lineages, and because they are arranged within a chronological time frame. Over the past 5 years I have begun to uncover an unexplored radiation of one of Hawaii's most abundant and conspicuous invertebrate groups: the spider genus *Tetragnatha*. The current study focuses on a small clade within the lineage, in which all the component species have abandoned web-building, instead foraging as cursorial predators. I examine 2 primary questions: 1. What has been the relative importance of strict geographic isolation (populations on different volcanoes) versus divergence between contiguous habitats (populations on the same volcano) in the evolution of this clade? 2. Does the phylogeny indicate a pattern of ecological and distributional change which could suggest that ecological rather than sexual shifts may underlie species formation? I generated a phylogeny based on morphological characters, and compared this phylogeny to the biogeographic pattern of the Hawaiian Islands. The results suggest that, for this clade of cursorial species, speciation requires strict geographic isolation, and ecological (more than sexual) shifts appear to play a role in initiating divergence. Considering the islands as a series of evolutionary snapshots, I would also speculate that speciation is commencing on the youngest island (Hawaii), and developing on the adjacent older island of Maui. □*Tetragnatha, phylogeny, Hawaii, speciation, allopatry.*

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Species represent one of the basic units of evolution, yet the processes by which they are formed remain poorly understood (Mayr, 1963). Studies of the Hawaiian biota have lent considerable insight into the mechanisms underlying speciation. These studies are highlighted by the Hawaiian *Drosophila*, in which sexual selection through female choice appears to play an integral role in inducing species formation among small populations colonizing geographically isolated islands (Carson, 1968; Carson and Kaneshiro, 1976; Kaneshiro, 1988). One may ask whether it is possible to generalize from these studies that adjustments in the sexual environment are largely responsible for driving species radiations. Other studies outside the Hawaiian Islands have found that ecological changes in isolation are more important in driving species proliferation (Mayr, 1963; Grant, 1986). When a species is released from interaction with related species, by whatever means, it may broaden its habitat use and exhibit much more variation among individuals (Lack, 1971; McCune, 1990). The argument is that if such a reproductively isolated incipient species were reunited with its parent, selection could act on the ecological variability to minimize the resources jointly used by both species, leading to further ecological divergence (Mayr, 1963; Grant, 1986).

The Hawaiian archipelago (Fig. 1) provides a natural laboratory for studies of speciation (Simon, 1987). First, the extreme isolation of the islands has allowed repeated and explosive diversification of species in a large number of lineages including honeycreepers (Berger, 1981; Freed et al., 1987), land snails (Cooke *et al.*, 1960), crickets (Otte, 1989) and drosophilid flies (Kaneshiro and Boake, 1987). Further, the islands are a series of volcanoes arranged within an identifiable chronological time frame; the currently high islands range from Kauai, the oldest and most eroded, to Hawaii, the youngest, highest and largest, with 5 separate volcanoes.

This study uses a lineage of spiders to examine speciation patterns within the context of the Hawaiian archipelago. The spiders belong to the long-jawed orb-weaving genus *Tetragnatha*, which comprises a large number of endemic species in the Hawaiian Islands (Gillespie, 1991, 1992). Outside the archipelago, *Tetragnatha* are among the most widespread and conspicuous spiders worldwide, yet collectively they are also

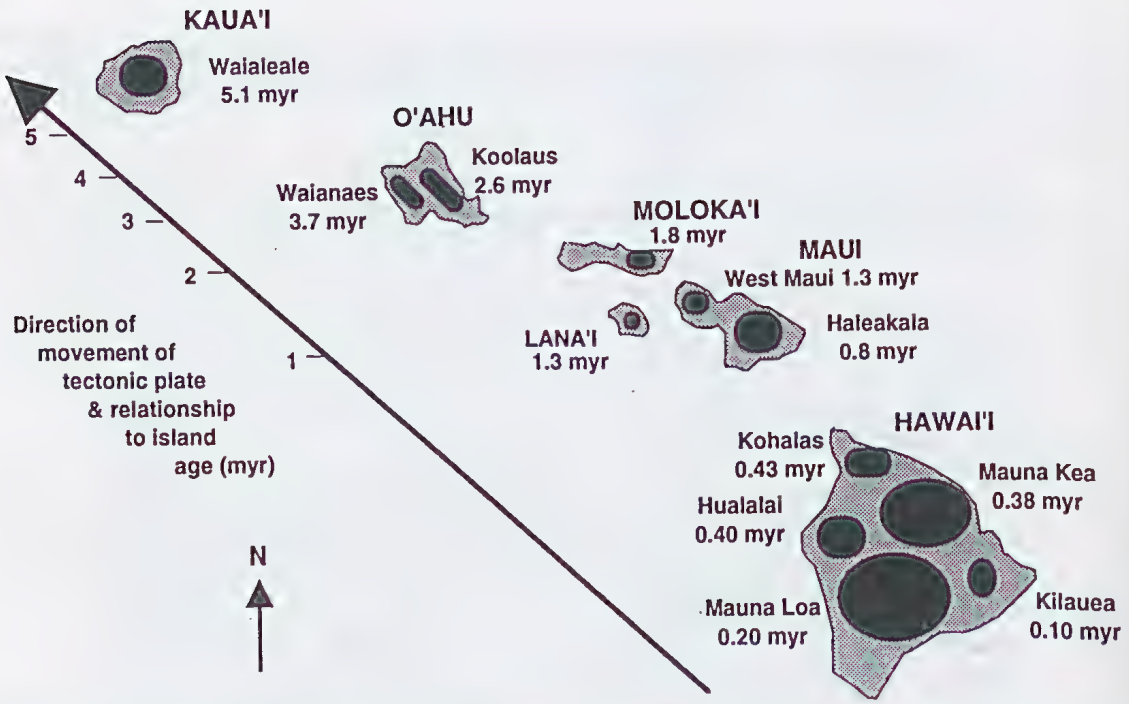

FIG. 1. Major land masses of the Hawaiian archipelago, indicating approximate age, and direction of movement of tectonic plate.

one of the most homogeneous, both in morphology (elongate bodies and long legs) and ecology (orb web generally built over or near water) (Wiehle, 1963; Levi, 1981; Gillespie, 1986, 1987). Hawaiian species of *Tetragnatha* represent a paradox, exhibiting considerable morphological and ecological diversity. Until 1992, the sole reference to endemic Hawaiian representatives of the genus was based on descriptions of a single species by Karsch (1880) and 8 species by Simon (1900, redescribed by Okuma, 1988). I have now described an additional 16 species (Gillespie, 1991, 1992), and have collected more than 60 new taxa that span a broad spectrum of colours, shapes, sizes, ecological affinities, and behaviours. In terms of courtship behaviour, however, Hawaiian representatives of the genus display the simple cheliceral locking mechanism characteristic of the genus (Levi, 1981; Gillespie, pers. obs.).

Here I examine a small clade (the 'spiny-leg' clade) within the radiation of Hawaiian *Tetragnatha*. Representatives of this clade are characterized by a cursorial habit, and do not build webs (Gillespie, 1991). Further, in common with other representatives of the genus (Levi, 1981), but in striking contrast to the *Drosophila* radiation, these spiders display minimal courtship behaviour. Because explanations for species formation in the Hawaiian *Drosophila* rely heavily on the elaborate courtship behaviour of the group, the absence of such behaviour in the Hawaiian *Tetragnatha* suggests that alternative explanations might be required to account for species proliferation. The questions I address in this study are: 1. What has been the relative importance of strict geographic isolation (taxa diverge on different volcanoes) versus divergence between contiguous habitats (taxa diverge on the same volcano) in the evolution of the spiny-leg clade of Hawaiian *Tetragnatha*? I generated a phylogeny for the clade based on morphological characters, and then compared the phylogeny to the biogeographic pattern and history of the islands. 2. Does the phylogeny indicate a pattern of ecological and distributional change which could suggest that ecological rather than sexual shifts may underlie species formation?

METHODS

Collection and Ecological Measurements

Spiders were collected by visual night searching at various times of the year between 1987 and 1991 in wet, mesic and dry native forest in all of the currently high Hawaiian Islands (Kauai,

Oahu, Molokai, Lanai, Maui and Hawaii; Fig. 1). Habitats from which spiders were taken were scored as wet (>450cm average annual rainfall), mesic (250-450cm) or dry (<250 cm). Elevation was categorized as low (<1000 m), medium-low (1000-1700m), medium-high (1700-2000m) and high (>2000m). Microhabitat associations were determined by categorizing the specific site from which an individual was collected (roots, fern fronds, against bark, etc.) (Gillespie, 1987).

Phylogenetic Analysis

I used a cladistic approach (Hennig, 1966) based on morphological characters to determine relationships among the spiny-leg clade of Hawaiian *Tetragnatha*. I scored a total of 30 characters relating to cheliceral armature (upper and lower tooth rows), leg spination, and colour of the cephalothorax and abdomen (Table 1). In addition, I scored characters from the detailed structure of the male palp using a Hitachi S-800 scanning electron microscope. I used a Hawaiian web-building species of *Tetragnatha*, *T. stelarobusta* Gillespie as an outgroup in the analysis because molecular data indicate that this species belongs to a closely related sister clade of the spiny-leg species (H.B. Croom, pers. comm.).

Characters were analyzed as unordered states (i.e., any character state permitted to transform directly into any other state) using Fitch (Fitch, 1971) and Wagner (Farris, 1970) parsimony in PAUP (Swofford, 1990) under the accelerated transformation method of optimization. Character states were polarized as primitive or derived by outgroup comparison (Maddison *et al.*, 1984), and characters were scaled for equal character weighting regardless of the number of states. A branch-and-bound search was conducted to find the shortest tree. The data were then reanalyzed by successive approximations, weighting characters according to their rescaled consistency index (Farris, 1969, 1989).

Relationship between Species Phylogeny and Island Biogeography

To test the importance of strict geographic isolation in initiating divergence, and the extent to which regular ecological and distributional changes have accompanied species formation, I compared the resulting phylogeny to the biogeographic locations of the component taxa within the Hawaiian archipelago.

RESULTS

Collection and Ecological Measurements

Representatives of the spiny-leg clade of Hawaiian *Tetragnatha* occur on each of the high islands. All are restricted to wet forest except for *T. brevignatha* Gillespie, *T. restricta* Simon and *T. quasimodo* Gillespie, which occur in wet, mesic, and sometimes dry, forest. The ranges over which the different species were found is listed in table 2. Microhabitat associations were loose, although the bright green species (*T. tantalus* Gillespie, *T. polychromata* Gillespie, *T. brevignatha*, *T. macracantha* Gillespie, *T. waikamoi* Gillespie and *T. kauaiensis*) were collected almost entirely from leaves, whereas the darker coloured *T. kamakou* Gillespie, *T. perreirai* Gillespie, *T. pilosa* Gillespie, *T. quasimodo* and *T. restricta* were collected from brown or red-brown substrates.

Phylogenetic Analysis

When characters were scaled for equal weighting regardless of number of states and unordered, a total of 7 most parsimonious trees were generated (consistency index 0.517, retention index 0.509). Subsequent weighting by successive approximations had little effect on the tree topology, and gave a single tree of unweighted length 76 (consistency index 0.725, retention index 0.765). Fig. 2 shows the tree with explanations of the characters defining each node. The characters defining species are marked as bars.

Relationship between Species Phylogeny and Island Biogeography

As can be seen from this phylogeny based on morphological characters (Fig. 2), the most closely related species are never found on the same island. The only regular pattern of ecological and distributional change through the Hawaiian Islands is the broadening habitat usage on the younger islands. In particular, taxa on the oldest islands (Kauai and Oahu) are all endemic to single volcanoes, while on the youngest island, Hawaii, there are no species endemic to the island, despite its much larger size (5 volcanoes). In addition, taxa on the youngest island occupy a much broader range of habitat types: *T. brevignatha*, for example, is found at all elevations and in dry, mesic and wet forest on Hawaii Island, whereas representatives of this species on East Maui occur only in mesic forest at middle elevations. Distributions of representatives of the clade on East Maui show some anomalies. In particular,

		stel	kau	pil	mac	pol	tant	wak	brev	perr	kam	rest	quas
1	♀ first tooth: tiny/moderate size/as large as others	1	1	1	1	1	1	2	1	1	1	1	0
2	♂ first tooth: absent /bump/finger	2	2	2	0	1	1	2	0	2	2	2	2
3	♂ 'sl' (first tooth down margin): bent up/straight/bent down	1	1	1	1	1	0	1	0	1	1	1	2
4	♂ 'sl' close to 'T' (second tooth down margin)?	0	0	0	0	0	0	0	0	0	1	1	1
5	♂ apical tooth (lower chelicera) present?	1	1	0	0	0	1	1	0	1	0	0	0
6	No. large teeth on lower margin ♂ chelicera: 1/ 2	0	1	0	1	1	1	1	0	1	1	0	1
7	♂ lower tooth row: short/ long	1	1	0	1	1	1	1	0	0	1	0	1
8	♂ teeth 3 and 4 on lower margin much smaller than rest?	1	1	1	0	1	1	1	1	0	1	1	1
9	♂ teeth 5 onwards larger than 3 and 4?	1	1	1	0	1	1	1	1	1	1	1	1
10	♂ first two teeth well separated?	1	0	1	1	1	1	0	0	0	0	0	0
11	Curl on terminal projection, conductor: none/ slight/ complete	0	1	1	1	0	2	2	1	1	1	2	0
12	Terminal projection of conductor points: straight/ backward/ forward	0	2	2	2	0	2	2	2	2	2	2	1
13	Cap of conductor tip: shallow/ deep	0	0	1	1	0	0	0	0	1	1	1	0
14	Cap ridge of conductor tip: lateral/ medial	0	0	0	0	0	1	1	0	1	0	0	0
15	Backward projection of conductor tip: above/ at same level/ below cap	0	0	0	1	1	0	0	0	1	1	1	1
16	Spur of conductor tip: indistinct/ prominant	0	1	1	1	1	1	1	1	1	1	1	1
17	Spur of conductor tip: angled up/ straight out/ hooked down	1	2	0	2	1	1	1	0	1	2	0	0
18	Floor and spur base of conductor tip: at same level/ separated	0	0	0	1	1	0	0	0	1	1	1	1
19	Separation of conductor cap and pleats: large/ small	1	0	0	0	0	0	0	0	0	0	0	0
20	Cap of conductor: wide/ medium/ high	0	0	0	2	0	0	0	0	1	2	2	0
21	Cap of conductor: rounded/ pointed right/ flat	0	0	2	0	0	1	1	2	0	0	0	2
22	Tip of conductor twists to show underside?	0	1	1	1	1	1	1	1	1	1	1	1
23	Venter color: translucent/ dark	1	0	1	0	0	0	0	0	1	1	1	1
24	Venter pattern: plain/ median bar/ paired spots.	1	1	2	1	1	1	1	0	0	0	1	1
25	Sternum color: translucent/ opaque	1	0	1	0	0	0	0	0	1	0	1	1
26	Orb webs built?	0	1	1	1	1	1	1	1	1	1	1	1
27	Tip of ♂ conductor projection: blunt/ pointed	0	0	0	0	1	1	1	1	1	1	1	1
28	Seminal receptacles: no swelling/swelling angled down/ angled up	0	2	0	2	0	2	2	2	1	1	2	2
29	Dorsum color: brown/ variable/ green	0	1	0	2	2	2	2	2	0	0	0	0
30	Tibial spines (lateral,medial, dorsal): 332/ 442/ 552	0	1	2	2	1	2	1	2	0	0	0	1

TABLE 1. Characters used for generating phylogeny. stel = *T. stelarobusta*; kau = *T. kauaiensis*; pil = *T. pilosa*; mac = *T. macracantha*; pol = *T. polychromata*; tant = *T. tantalus*; wak = *T. waikamoi*; brev = *T. brevignatha*; perr = *T. perreirai*; kam = *T. kamakou*; rest = *T. restricta*; quas = *T. quasimodo.*

there are three bright green species, one endemic to this volcano (*T. macracantha*), one shared with West Maui (*T. waikamoi*) and *T. brevignatha* shared with Hawaii Island. The East Maui species exhibit parapatric ranges, with only very narrow zones of overlap, and are more closely related to species on other islands rather than to each other.

DISCUSSION

Differentiation between species of the spiny-leg clade of Hawaiian *Tetragnatha* appears never to have occurred on the same mountain mass: in no situation are two sister species found on the same volcano, or even on the same island. This phylogeny based on morphological characters therefore strongly suggests that strict geographic isolation (between islands only) is necessary for the initiation of species formation. Such isolation appears also to underlie speciation events in the Hawaiian *Drosophila* (Carson and Templeton, 1984). The phylogeny of the Hawaiian spiny-leg *Tetragnatha* also indicates that species colonize in a generally southerly direction, with the most ancestral taxa occupying the oldest island, Kauai. In addition, colonization of the most recent island (Hawaii) may be associated with ecological release: populations of each of the three species that have colonized Hawaii Island, *T. quasimodo*, *T. restricta* and *T. brevignatha*, occupy a broad

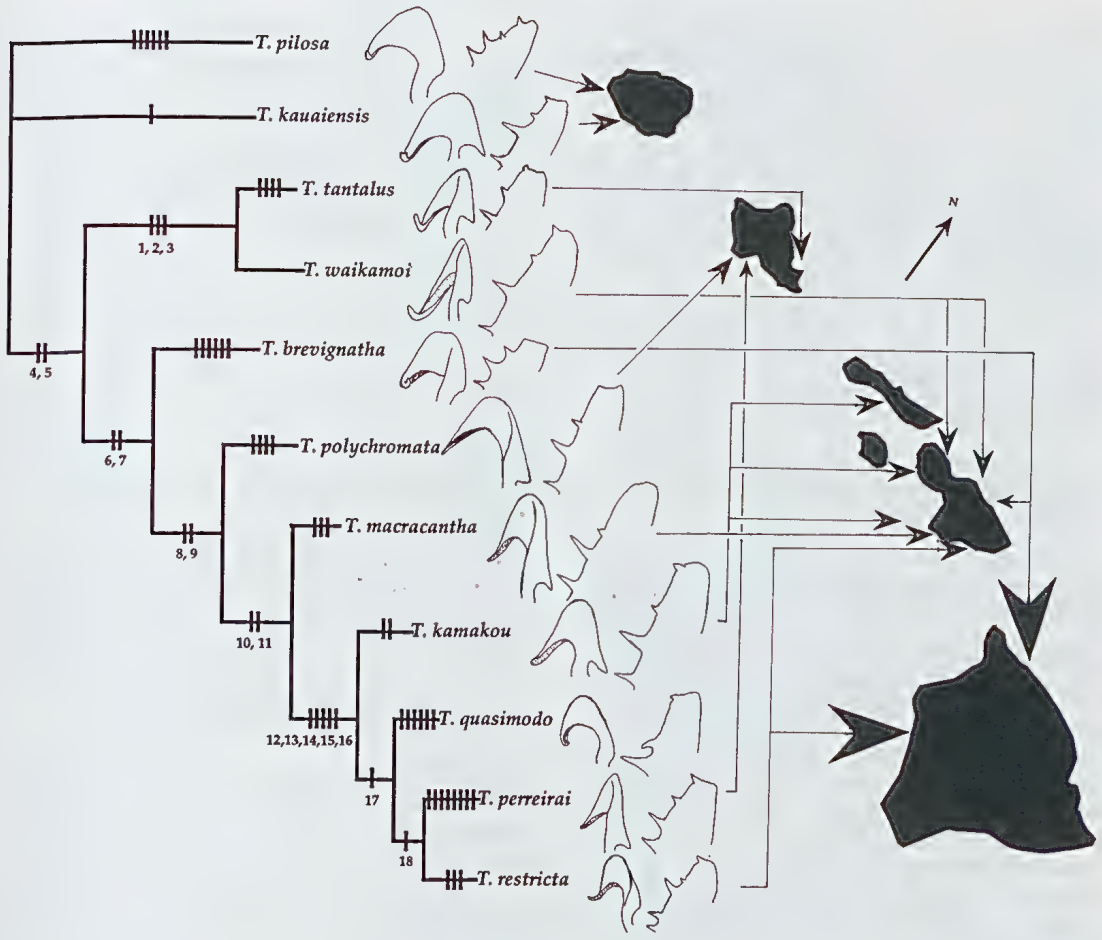

FIG. 2. Phylogeny of the Hawaiian spiny-leg *Tetragnatha* based on morphological characters. Explanations are given for characters defining each node; characters defining species are marked as bars. Sketches of the tip of the male conductor (left) and the upper surface of the apical portion of the male chelicera (right) are included for ease of comparison. Arrows point to the location of a species in the archipelago, with the size of an arrow tip being approximately proportional to the size of the distribution of a given species.Character changes defining each node are as follows. **1**, Conductor terminal projection: short->long. **2**, Conductor cap ridge: lateral–>medial. **3**, Conductor cap: rounded–>pointed. **4**, Conductor cap tip: blunt–>pointed. **5**, Colour: brown/variable–>green. **6**, First upper cheliceral tooth lost. **7**, First lower cheliceral tooth lost. **8**, First 2 lower margin cheliceral teeth–> well separated. **9**, Conductor backward projection at level–> below cap. **10**, Conductor cap: low–>high. **11**, Backward projection conductor spur–>angled down. **12**, Venter: pale–>dark. **13**, Abdomen colour: green–>brown. **14**, First dorsal cheliceral tooth–>finger. **15**, Cheliceral 'sl' tooth–> closer to 'T'. **16**, First 2 lower cheliceral teeth–> closer. **17**, Conductor backward projection hooked up–> angled down. **18**, Lower tooth row long–> short.

range of habitat types. In particular, *T. brevignatha* is found in almost every habitat type on Hawaii Island, whereas representatives of the species on East Maui are confined to a narrow band of mesic forest at middle elevation.

There are some distinct differences between the pattern of phylogeny I have generated here for the Hawaiian *Tetragnatha* and patterns suggested for the Hawaiian *Drosophila*. The Hawaiian *Drosophila* generally demonstrate single volcano endemism, one species having its closest relatives on an adjacent volcano. In contrast, the phylogeny I have generated for the spiny-leg species of Hawaiian *Tetragnatha* suggests a non-uniform and disjunct pattern. Possible explanations for the *Tetragnatha* pattern may best be

ISLAND	HAWAII											MAUI						MO	LA	OAHU			KA
VOLCANO	Mauna Loa							M. Kea		Kh	Hu	W	Haleakala					Ka	La	Wainaes		Ko	Wai
	S	W	W	E	E	Saddle		E	E				N	N	E	E	W						
Elevation	1-2	0-1	1-2	0-1	1-2	0-1	1-2	0-1	1-2	1-2	1-2	1-2	0-1	1-2	0-1	1-2	1-2	1-2	1-2	0-1	1-2	0-1	1-2
tantalus																						X	
polychromata																				X	X		
brevignatha		X	X		X		X	X	X	X	X			X									
macracantha													X		X	X							
waikamoi												X		X	X	X							
kauiensis																							X
kamakou												X		X		X							
perreirai																					X		
pilosa																							X
quasimodo	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X		X	X	X			

TABLE 2. *Tetragnatha* species collected at different sites (islands, volcanoes and elevations, x 100m) through the Hawaiian Islands. Islands: MO= Molokai; LA= Lanai; KA= Kaui. Volcanoes: M. Kea= Mauna Kea;Kh= Kohala; Hu = Hualalai; W= W. Maui; Ka= Kamakou; La= Lanaihale; Ko= Koolaus; Wai = Waialeale.

considered by viewing the Hawaiian archipelago as a series of evolutionary snapshots, with speciation starting on Hawaii Island and developing on East Maui. The three species on the recently formed Hawaii Island are likely to be relatively recent colonists that have expanded their range and habitat use. Such ecological release subsequent to colonization is considered an important step in initiating species divergence in Galapagos finches (Grant, 1986). However, the widespread species on Hawaii Island are remarkably homogeneous, and none are endemic to the island. It may be that Hawaii Island is too young for speciation to have occurred in the spiny-leg Hawaiian *Tetragnatha*. The situation suggests that considerable movement of individuals occurs within the island, and gene flow between islands has been sufficient to prevent speciation during the period of existence of Hawaii Island.

The adjacent older volcano of East Maui was once part of the island complex, 'Maui Nui' (comprising Molokai, Lanai, East and West Maui). This island was likely first invaded by *T. tantalus*. Males may be better colonists than females (Bishop, 1990), but spiderlings would also arrive, and eventually give rise to a population that would expand its range on that island. However, colonists would continue to arrive on Maui Nui, and, at least initially, the original colonists would not be reproductively isolated from the secondary colonists of the same species. It is also possible that, if the secondary colonists included closely related heterospecifics, hybridization might occur, as newly forming taxa tend to have poorly developed sexual discrimination (Kaneshiro, 1976, 1983; Carson *et al.*, 1989). Indeed, it is possible that both *T. macracantha* and *T. brevignatha* arose through hybridization, which may play an important element in the formation of species in general (Endler, 1989).

As sexual discrimination and ecological adaptation develop, invaders would presumably lose their ability to colonize an occupied land mass. The pattern of distribution of representatives of the spiny-leg clade on older islands suggests that closely related taxa cannot maintain coexistence on the same land mass unless they have undergone sufficient ecological divergence. The situation on East Maui may therefore represent an unstable state: ultimately, a single species will take over the land mass, as a result of introgression or competitive displacement.

The mechanism I have proposed for speciation among representatives of the spiny-leg Hawaiian *Tetragnatha* remains speculative. However, the repeated ecological release of newly forming taxa strongly suggests that ecological changes have played some role in initiating species divergence, as does the finding that two populations (Maui versus Hawaii) of an apparently diverging species (*T. brevignatha*) differ only in terms of their habitat occupation. I suggest that, unlike the Hawaiian *Drosophila* in which sexual selection has been heavily implicated in the speciation process (Kaneshiro, 1983; Kaneshiro and Giddings, 1987), ecological factors (range expansion, reinvasion, competition) may be more important among the spiny-leg species of Hawaiian *Tetragnatha*.

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A NEW SPECIES OF KARSCHIIDAE (SOLIFUGAE, ARACHNIDA) FROM KAZAKHSTAN

ALEXANDER V. GROMOV

Gromov, A.V. 1993 11 11: A new species of Karschiidae (Solifugae, Arachnida) from Kazakhstan. *Memoirs of the Queensland Museum* **33**(2): 527-528. Brisbane. ISSN 0079-8835.

The new solpugid species *Karschia mangistauensis* of the family Karschiidae is described from material collected in south-western Kazakhstan. The relationship of the new species is given, as well as the list of solpugids currently known from Kazakhstan.
En se basant sur le matériel récolté au Sud-Ouest du Kazakhstan on décrit une nouvelle espéce de solifuge *Karschia mangistauensis* de la famille Karschiidae. On donne les affinités de la nouvelle espéce aussi que la liste des solifuges connues à présent au Kazakhstan.□*Solpugids, Karschiidae, Karschia, Kazakhstan.*

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The solpugid fauna of Kazakhstan is poorly known. Only 13 species were recorded from the region by Birula (1938): these are *Karschia zarudnyi* Birula, *Eusimonia turkestana* Kraeplin, *Anoplogylippus dsungaricus* Roewer, *A. rickmersi* (Kraeplin), *Hemigylippus lamelliger* Birula, *Galeodes araneoides* Pallas, *G. turkestanus* Kraepelin, *G. caspius* Birula, *G. fuscus* Birula, *G. pallasi* Birula,*Paragaleodes heliophilus* Heymons, *P. pallidus* Birula and *Daesia rossica* Birula.

The present paper concentrates on material collected from Mangyshlak and Ustyurt Plateaus (south-western Kazakhstan). Solpugids were preserved and studied in 70% alcohol using a binocular microscope MBS-1. Their determination was done according to Walter (1889), Birula (1938) and Roewer (1932-1934, 1941).

MORPHOLOGY AND BIOLOGY
Family KARSCHIIDAE

Karschia mangistauensis sp. nov.
(Figs 1-10; table 1)

Material Examined

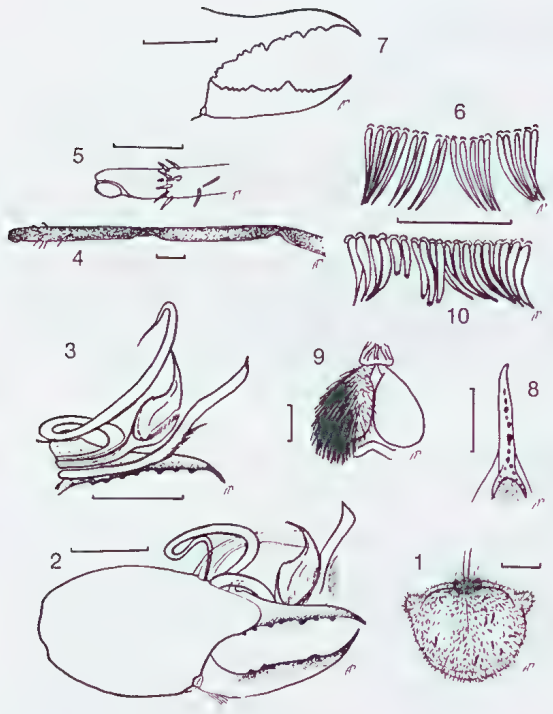
TYPES. Holotype ♂, Zhylandy Cape, Yeraliev District, Mangyshlak Plateau, Mangistau Area, South-Western Kazakhstan, (43°06'N, 51°39'E), 2 May 1991, A.V. Gromov. Paratypes: South-Western Kazakhstan: Mangistau Area: Mangyshlak Plateau: 2 ♂, 2 ♀, same data, except 2-4 May 1991, K.U. Balmukanov, A.V. Gromov, K.B. Dzhankurazov; 1 ♂, Aktau City [Shevchenko], (43°11'N, 51°39'E), 28 April 1991, K.U. Balmukanov; Ustyurt Plateau: 1 ♂, Kugusem Well, 68.5 km E of Akkuduk Village, Yeraliev District, (43°10'N, 54°53'E), 2-5 May 1990, S.I. Ibraev; 1 ♀, Sulykkyzylsai Well, 69.5 km NE of Akkuduk Village, Mangistau District, (43°28'N, 54°43'E), 12 May 1991, E.E. Kopdykbaev. Holotype and 1 ♀ paratype preserved in Zoological Institute, St Petersburg [Leningrad], the remaining material in the author's collection.

Diagnosis

The new species is closely related to *Karschia cornifera* Walter, 1889 from Turkmenistan, from which it differs by the colouration, by the shape of upper modified mesolateral seta near the base of cheliceral fingers, by the number of teeth on the fixed finger and by the spinulation of pedipalps.

Description

Male (holotype). Total length 21 mm. Body colouration light yellow-brown, with greyish head and thorax and grey-yellow abdomen with darker tergites. Chelicerae yellow, distally including brownish-black teeth. Pedipalps (Fig. 4): proximal part of femur yellow, distal part of femur and the remaining segments greyish. Legs yellow. Ocular tubercle (Fig. 1) dark, with numerous hairs, sparse short setae and 2 long setae. Near the base of the cheliceral fingers there is a mesal row of long setae: the upper two are strongly modified and thickened (Figs 2, 3). Armature of pedipalps (Fig. 5): protarsus (basitarsus, metatarsus auct.) with 9 promesolateral spines, tarsus with 1 mesobasal spine. Third abdominal segment with 46 broad ctenidia, fourth one with 19 ctenidia (Fig. 6).



FIGS 1-10. *Karschia mangistauensis*, sp. nov. 1-6, male; 7-10, female. 1, propeltidium, dorsal view. 2, right chelicera, ectal view. 3, modified setae near base of fingers, and flagellum on left cheliceral fixed finger, mesal view. 4, 5 right pedipalp, mesoventral view; coloration (4); spinulation (5). 6, ctenidia on fourth sternite of abdomen, ventral view. 7, right chelicera, ectal view. 8, right cheliceral fixed finger, ventral view. 9, genital opercula, ventral view. 10, ctenidia on fourth sternite of abdomen, ventral view. Scale line = 1 mm.

Body length of paratypes 17-21 mm, number of promesolateral spines 6-10, mesobasal spine of tarsus sometimes absent, fourth abdominal segment with 17 or 19 ctenidia.

Female paratype. Body colouration lighter than in male, with darker pedipalps. Distal part of femur IV light brown. The head behind ocular tubercle with slight longitudinal light brown line. Ocular tubercle as in male, occupying less than 1/3 of clypeus width. Fixed fingers are straight from above, their length no more than the width of chelicerae. Armature of chelicerae as in Figs 7, 8. Genitalia (Fig. 9) with pale rosy ectolateral setae. Fourth abdominal segment with 19 pale rosy ctenidia which are thicker than in male (Fig. 10).

	Length
Chelicerae	4.4, 1.6 wide
Propeltidium	2.4, 3.5 wide
Pedipalp: total (with coxa)	18.2
tibia	4.9
basitarsus	3.8
Leg I (with coxa)	14.1
Leg II (with coxa)	12.4
Leg III (with coxa)	16.6
Leg IV (with coxa)	25.3

TABLE 1. Measurements (in mm) of *Karschia mangistauensis*, sp. nov.

Biology

Night solpugid in clayey desert under stones during day.

ACKNOWLEDGEMENTS

I am grateful to Messrs K.U. Balmukanov and K.B. Dzhankurazov (Kazakh State University, Alma-Ata) for their assistance in capturing of the new species, Mr S.I. Ibraev and Mr E.E. Kopdykbaev (Institute of Zoology, Kazakhstan Academy of Sciences, Alma-Ata) for their material kindly presented to me, and to Dr A.A. Zyuzin (Institute of Zoology, Kazakhstan Academy of Sciences, Alma-Ata) for translation of manuscript. I am also indebted to Dr Ch. K. Tarabaev (Institute of Zoology of Kazakhstan Academy of Sciences, Alma-Ata) who presented my paper at the XII International Congress of Arachnology (Brisbane, Australia).

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A NEW SPECIES OF *AMAURORIOIDES* O.P.-CAMBRIDGE (ANYPHAENIDAE: ARANEAE) FROM SOUTH AUSTRALIA

D.B. HIRST

Hirst, D.B. 1993 11 11: A new species of *Amaurobioides* O.P.-Cambridge (Anyphaenidae: Araneae) from South Australia. *Memoirs of the Queensland Museum* **33**(2): 529-532. Brisbane. ISSN 0079-8835.

The littoral spider *Amaurobioides isolatus* sp. nov. is described from South Australia and is the first new species of the genus from the Australian mainland. The male palp of *A. litoralis* Hickman is re-illustrated. Biogeography is discussed. □*Araneae, Anyphaenidae, Amaurobioides, new species.*

David B. Hirst, South Australian Museum, North Terrace, Adelaide, South Australia 5000, Australia; 6 November, 1992.

The genus *Amaurobioides* O. Pickard-Cambridge, 1883 occurs in New Zealand (Cambridge, 1883), Campbell Island (Hogg, 1909), South Africa (Hewitt, 1917) and was reported from Tasmania (Hickman, 1949) and Chile (Forster, 1970). Forster (1975) included the south-east coast of Australia in the distribution of the genus but that was not cited by Main (1981) or Davies (1986). The specimen(s) to which Forster (1975) referred were deposited in the Australian Museum, Sydney (AM) but were not labelled as *Amaurobioides* (unpublished data) and have not been found (pers. comm., M. Gray). No further material has been reported from mainland Australia. Once *Amaurobioides* was found on the rocky shoreline of the eastern side of Gulf St Vincent in South Australia , deliberate searching in similar habitats on Eyre Peninsula, Fleurieu Peninsula and Kangaroo Island showed the species was widespread.

Types of *A. litoralis* Hickman, 1949 (syntype series of 1 ♂ and 3 ♀♀ from Tasmania) deposited in AM, were examined. Hickman made no special type designations but the male seen (AM KS6410) is labelled 'Holotype'. Hence, the label designation is invalid (Art. 73iii). The series also includes two females of an undescribed species (Forster, 1970). Forster, when noting that this type material comprised two sympatric species, stated that the larger form was *A. litoralis* while the smaller form was undescribed.

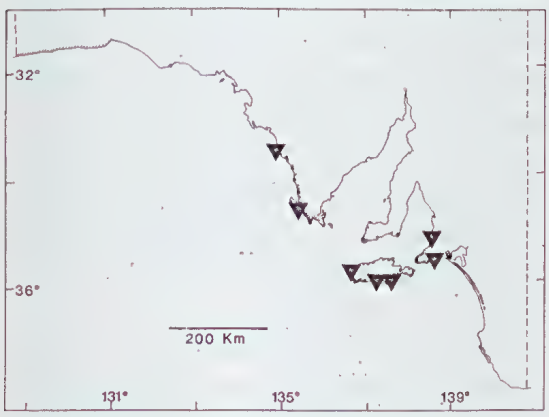


FIG. 1. Southern portion of South Australia showing the distribution of *Amaurobioides isolatus*. Shaded coastline may include suitable habitats.

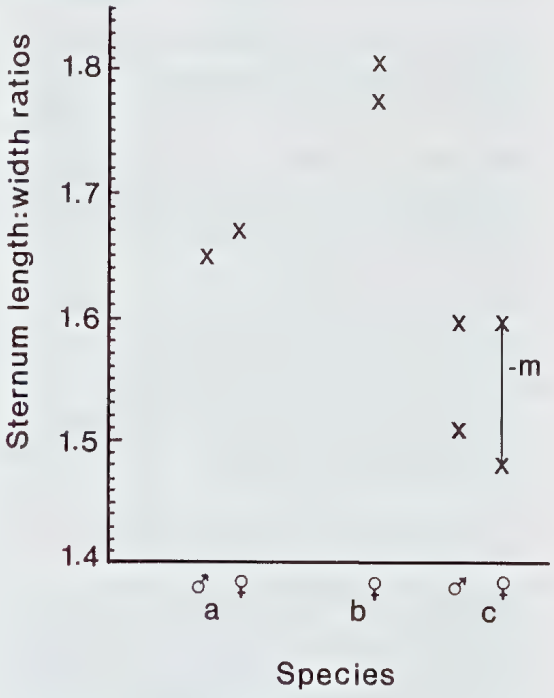


FIG. 2. Comparison of sternum length: width ratios: a, b, *A. litoralis*: small form (a); large form (b); c, *A. isolatus*. m, mean.

FIG. 3. *A. litoralis*. Tibial apophysis and cymbium of syntype ♂ AM KS6410, ventral.

The ♂ is similar in size to the sole smaller ♀ of the type series, and not to the two larger ♀♀ as suggested by Forster (also captions for figures of the two forms appear to be transposed as the larger specimen figured is called the small form). This is supported by comparisons of the sternum length:width ratio (Fig. 2). Ratios: ♂, 1.65 and smaller type ♀ 1.67; larger ♀♀, 1.77, 1.81; ♀ *A. isolatus* 1.48-1.60 (n=14, mean =1.56) and 2 ♂♂, 1.51, 1.60. Although based only on Australian material seen, the conspecific ♂ of the larger and undescribed form would probably attain a ratio in excess of 1.70.

The ♂ palp of *A. litoralis* is re-illustrated here; the ♀ epigynum was adequately illustrated in Forster (1970, figs 487, 488).

METHODS AND MATERIALS

Hairs are omitted from illustrations. ♀ genitalia were dissected then cleared in lactic acid. All measurements are in millimetres. *Abbreviations*: CL, carapace length; CW, carapace width; AL; abdomen length; AW, abdomen width, MOQ, median ocular quadrangle; aw, anterior width; pw, posterior width; L or l, length, W, width; K.I., Kangaroo Island; DH, D. Hirst.

Amaurobioides isolatus sp. nov.
(Figs 1, 2, 4-9, Table 1)

Material Examined

TYPES. Holotype ♂, Blanche Point, 35°15'S, 138°28'E, 1.iii.1986, DH, N1992206. Paratypes: allotype ♀, same data as above, N1992207; ♀ (with spiderlings), Elliston, 33°39'S, 134°53'E, 31.iii.1987, DH, D. Lee, N1992218; ♀, juv., same data, N1992216-7; ♀, 5 penult. ♂, 2 penult. ♀, same data as holotype but 25.i.1986, N1992208-15; penult. ♀, Petrel Cove, 35°36'S, 138°36E, 1.ii.1991, DH, N1992219; ♀, 4 juv., Point Avoid, 34°41'S, 135°19'E, 31.iii.1987, DH, D. Lee, N1992221; ♀ (with spiderlings), juv., same data, N1992220; 2 ♀, juv., Point Ellen, K.I., 36°00'S, 137°11'E, 10.xi.1987, DH, N1992222-3; ♀ (with eggsac), Point Tinline, K.I., 35°59'S, 137°37'E, 11.xi.1987, DH, N1992224; ♂♀, Port Willunga, 35°16'S, 138°28'E, in retreats 0.5m above base of large rock on beach, 14.vi.1992, DH, N1992234-5; 4 ♀, juv., West Bay, K.I., 35°54'S, 136°32'E, 6.xi.1987, D, N1992225-9. All in South Australia and deposited in South Australian Museum.

Diagnosis

The ♂ of *A. isolatus* is recognised by the shape of the primary conductor. *A. isolatus* further differs from the two Tasmanian species in having the sternum relatively broader while the ♀ epigynum is smaller and less sclerotised. The ♂ has spination of tibia I identical to the ♀, a feature shared with *A. maritimus* O.P.-Cambridge, from which it is separated by the genitalia.

Description

MALE. CL 3.79, CW 2.56. AL 4.48, AW 2.41.

Colour in alcohol: Carapace yellow-brown, yellow posterior to fovea and laterally to above anterior legs, caput dark orange-brown, clypeus and lateral edge of face brown. Chelicerae red-brown, darker distally. Maxillae and labium orange-brown, anterior margins cream. Sternum cream, margins orange. Legs cream-yellow, anterior metatarsi and tarsi darker, coxae cream. Palp cream, cymbium brown. Abdomen cream with dark red-brown pattern dorsally and laterally, typical for genus. Venter darker around spiracle and posteriorly to spinnerets, dark area extending anteriorly from spiracle in two narrow lines almost to epigastric furrow.

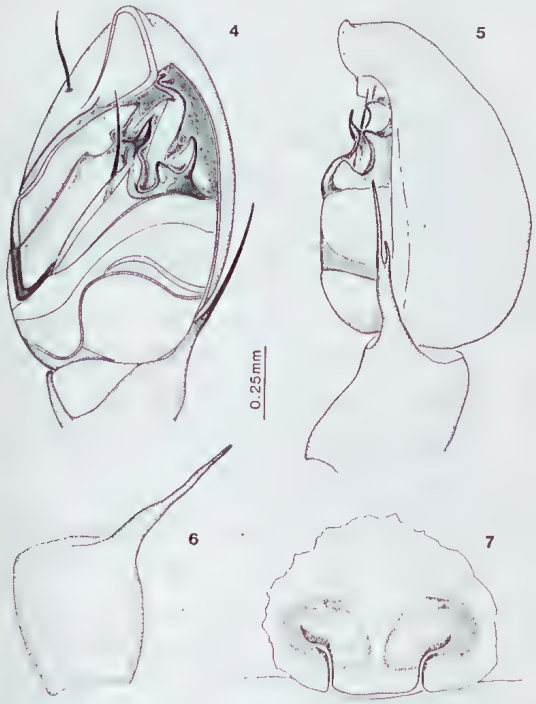
Carapace elongate, longer than broad in ratio 19:13, short imperfect longitudinal fovea [presumably straight in normal specimens]. Striae barely evident, adpressed setae black, upright setae on caput between fovea and ocular region. Eye group occupies less than half width of caput. AME 0.10, ALE 0.17, PME = PLE 0.18.

	Leg 1	Leg 2	Leg 3	Leg 4	Palp
Fe	3.32(2.67)	3.30(2.61)	2.71(2.46)	2.98(2.51)	1.50(1.40)
Pa	1.53(1.59)	1.56(1.48)	1.33(1.39)	1.47(1.50)	0.59(0.65)
Ti	3.40(2.50)	3.23(2.43)	2.24(1.82)	2.74(2.32)	0.65(0.66)
Me	3.19(2.34)	2.99(2.25)	2.40(1.96)	2.59(2.15)	- (-)
Ta	1.67(1.42)	1.42(1.29)	1.02(0.95)	0.97(0.95)	1.26(1.24)
Total	13.11(10.52)	12.50(10.06)	9.70 (8.58)	10.75 (9.43)	4.00 (3.95)

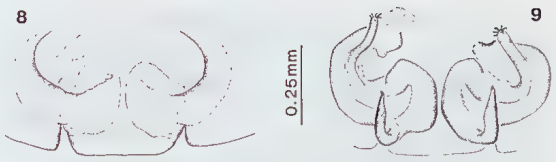
TABLE 1. Leg lengths of *Amaurobioides isolatus*. Values are for holotype ♂ (allotype ♀).

Interspaces: AME-AME 0.05, AME-ALE 0.04, PME-PME 0.11, PME-PLE 0.12, AME-PME 0.14, ALE-PLE 0.08. MOQ; aw: pw: l = 0.26: 0.47: 0.39. Width of clypeus to AME 0.10. Chelicerae with three teeth on both margins. Sternum: L 2.12, W 1.40. Legs. (Table 1) Scopula sparse, particularly on posterior pairs. Leg spination; no spines on patellae or tarsi. Ventral tibiae and metatarsi spines usually paired, occasionally single. Leg I, fe d3 p1, ti v6, me v3. Leg II, fe d3 p1, ti p1 v6, me v4. Leg III, fe d3 p1 r1, ti p1 r1 v5 (v6 on right), me p3 r3 v6. Leg IV, fe d3 p1 r1, ti r1 v3, me p2 r2 v5. Palp, fe d3 p1, pa with one stout bristle dorsally at distal end, ti many long stout bristles, cymbium with three short weak spines prolaterally.

Palp. Tibia with left apophysis having short dorsal median secondary prong (Fig. 5), right apophysis lacking accessory prong (Fig. 6), possibly normal state.



FIGS 4-7. *A. isolatus*. 4-5, Left tibial apophysis and cymbium of holotype ♂, 4, ventral, 5, retrolateral; 6, right tibia and apophysis; 7, epigynum of allotype ♀.



FIGS 8-9. *A. isolatus*. 8-9, cleared vulva of paratype ♀ N1992208, 8, ventral, 9, dorsal.

FEMALE (as ♂ except as follows).CL 4.21, CW 2.89. AL 6.97, AW 4.16.

Eyes. AME 0.11, ALE 0.20, PME 0.19, PLE 0.20. Interspaces; AME -AME 0.08, AME-ALE 0.06, PME-PME 0.12, PME-PLE 0.14, AME-PME 0.17, ALE-PLE 0.10. MOQ; aw: pw: l = 0.29: 0.50: 0.46. Width of clypeus to AME 0.06. Sternum: L 2.30, W 1.48. Legs. (Table 1)

Epigynum. Fossa broad, anterior margins vaguely defined by what appears to be subcuticular sclerotisation of vulva (Fig. 7). Vulva of paratype N1992208 shown in Figs 8, 9 [allotype not dissected].

Variation

CL of paratype ♂, 3.48; the tibial apophysis of both palps lack accessory prongs and the fovea is straight. CL of paratype ♀; 3.22-4.74, mean 4.35 (n=13).

Etymology

The specific epithet, *isolatus*, reflects the isolated nature of the species distribution.

NATURAL HISTORY

Habits are similar in other *Amaurobioides*. Silk retreats are assumed to be permanent although many spiders collected or observed at Blanche Point in February were wandering over the rocks at night. Several penultimate ♂♂♀♀ were collected in this way and kept alive for some time, one ♂ eventually maturing 3 months later. Most insects placed with the spiders, including moths and terrestrial isopods, were not fed upon. Small flies (mostly *Drosophila*) were more readily accepted (Forster, 1970: 167). Littoral isopods were not tried as a food source (Hickman, 1949). Since then a specimen of *A. isolatus* at Blanche Point lunged at and grasped a small littoral isopod half its size with its anterior legs, hesitated and then released the isopod, retreating to its position at the entrance to the nest. Small flies, often seen resting

in sheltered areas at night along the coast, are another likely food source. Females with spiderlings (26 and 42) in the retreat were found in mid-autumn at both Point Avoid and Elliston while spiderlings and an eggsac were found in separate retreats in November on Kangaroo Island.

BIOGEOGRAPHY

Most areas sampled were within the splash zone on rock faces sheltered from the full velocity of the sea, but retreats were seen in an exposed and treacherous area at Cape du Couedic, Kangaroo Island. Known populations are separated by unsuitable or sandy coastline of varying lengths (Fig. 1). *Amaurobioides* may have dispersed across the intervening ocean by parachuting on silk lines or drifting on flotsam to settle and inhabit their present littoral environments. Forster (1970) considered that claim to be overstated as a number of distinct forms, some sympatric, were present in New Zealand. Platnick (1976) reinforced that in the Laroniinae.

Since Australia's separation and subsequent drift from the other continents of Gondwanaland, the South Australian coastline has been altered by changes in sea level during the last ice-age. The rocky cliffs of Blanche Point and southern coast of Kangaroo Island which now provide a habitat for *Amaurobioides* were formed during the last ice-age over Tertiary deposits and have since been uplifted and weathered (Daily *et al.*, 1979). One population in D'Estrees Bay, Kangaroo Island, consisted of only a few individuals on a small isolated rock outcrop backed by a low sandstone ledge. Similarly, near Port Willunga and 2km south of Blanche Point, individuals exist on a few older limestone rocks remaining on the wide sandy beach which are reached by the normal high tide. Although backed by cliffs, no spiders were found on these. Cliffs also abut the sea in areas north of Blanche Point to Marino Rocks but as yet *Amaurobioides* has not been found. *Amaurobioides* is unlikely to be found from Victor Harbour on the Fleurieu Peninsula to at least Robe in the south-east of South Australia. Extensive sand dunes which now form the Coorong and much of the coast to the south are part of that area built up during inundation by the sea in the Miocene and the Pleistocene, and the few rocky outcrops now present have remained isolated since.

In summary, *Amaurobioides* is one of the few true Gondwanan spider genera left in South Australia presumably because continual changes to the coast have occurred gradually. Littoral spiders have moved with it through dispersal and colonising adjacent new areas of rocky terrain or re-establishing itself into old areas within a suitable distance from the receding or insurgent sea. The sympatry of species of *Amaurobioides* in New Zealand and Tasmania probably occurred by migration over land following uplift or weathering of unsuitable coastline between two separated species and exposing a continuous rocky habitat, rather than by dispersal on silk lines.

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I am grateful to Dr M. Gray (AM) for the loan of types of the Tasmanian *Amaurobioides* and to Mr L.N. Nicolson for commenting on an early draft of the manuscript.

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IMPLICATIONS OF THE PHYLOGENY OF PIMOIDAE FOR THE SYSTEMATICS OF LINYPHIID SPIDERS (ARANEAE, ARANEOIDEA, LINYPHIIDAE)

GUSTAVO HORMIGA

Hormiga, G. 1993 11 11: Implications of the phylogeny of Pimoidae for the systematics of linyphiid spiders (Araneae, Araneoidea, Linyphiidae). *Memoirs of the Queensland Museum* **33**(2): 533-542. Brisbane. ISSN 0079-8835.

The araneoid family Pimoidae (new rank) is hypothesized to be the sister group of Linyphiidae. *Louisfagea* Brignoli is a junior synonym of *Pimoa* Chamberlin and Ivie (new synonymy). The characters that support the monophyly of Pimoidae and of Linyphiidae plus Pimoidae are discussed. Explicit outgroup comparison to the closest relatives of linyphiids (i.e., pimoids) allows studies of character evolution and character polarization within linyphiids and the assessment of previous phylogenetic hypotheses for the family. Preliminary data on the implications of pimoid phylogeny for linyphiid systematics are evaluated, based mainly on morphological characters. Linyphiid monophyly is discussed.

La familia araneoide Pimoidae (nuevo rango) es, hipotéticamente, el grupo hermano de Linyphiidae. El género *Louisfagea* Brignoli se considera sinónimo de *Pimoa* Chamberlin and Ivie (nueva sinonimia). Se discuten los caracteres que apoyan la monofilia de Pimoidae y de Linyphiidae más Pimoidae. La utilización explícita del criterio de comparación con el grupo externo de los linífidos (es decir, los pimóidos) permite estudiar la evolución y polarización de caracteres en linífidos, así como la evaluación de anteriores hipótesis filogenéticas sobre esta familia. Se evaluan los datos preliminares, basados en caracteres morfológicos principalmente, sobre las implicaciones de la filogenia de los pimóidos para la sistemática de los linífidos. También se discute la monofilia de Linyphiidae. □*Pimoidae, Linyphiidae, Pimoa, cladistics, phylogeny, monophyly, homology.*

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Linyphiids are one of the dominant spider groups in the Holarctic region. Despite their overwhelming diversity and involved taxonomic history the phylogenetic structure of the family and their relationship to other araneoids are very poorly understood. In this paper I present some preliminary data on the systematics of pimoids, confirming their sister-group relationship to linyphiids, and on the cladistic structure of a small sample of linyphiid genera. A revision and numerical cladistic analysis of the pimoids and the sample of linyphiid taxa (Hormiga, in press), together with detailed character information, will be published elsewhere shortly. The study of the phylogeny of the pimoids requires the inclusion of at least a sample of linyphiids (their putative sister-group) in order to assess character state polarities by means of outgroup comparison. It is in such a context that the present study should be considered, since the small sample of genera used here can by no means account for the whole range of linyphiid diversity. However, quantitative cladistic analysis of the data presented here enables for some testable hypotheses on linyphiid systematics and character evolution, by explicitly stating phylogenetic relationships in terms of synapomorphies rather than by the more speculative approaches that have commonly been used in traditional linyphiid higher systematics. This approach enables us to evaluate comparative morphological data (or any other kind of biological data) in a cladistic context. Hypotheses on phylogeny and character homology hypotheses are indistinguishable because 'every hypothesis of homology is a hypothesis of monophyletic grouping' (Patterson, 1982). Finally, the present study allows for a preliminary test of the phylogeny of the linyphiid subfamilies proposed by Wunderlich (1986).

MATERIALS AND METHODS

Taxa

Nine linyphiid, five pimoid, and two non-linyphiid araneoid genera that are possible outgroups of the pimoid-linyphiid complex are used in this study. The linyphiid taxa selected represent the subfamilies and tribes used by Wunder-

lich (1986) in his phylogenetic scheme for Linyphiidae (given here in parentheses): *Linyphia triangularis* (Clerck) and *Microlinyphia dana* (Chamberlin and Ivie)(Linyphiinae, Linyphiini); *Bolyphantes luteolus* (Blackwall) and *Lepthyphantes tenuis* (Blackwall)(Linyphiinae, Micronetini); *Erigone psychrophila* Thorell and *Walckenaeria directa* (O.P.-Cambridge) (Erigoninae); *Haplinis diloris* (Urquhart) and *Novafroneta vulgaris* Blest (Mynogleninae); and *Stemonyphantes blauveltae* Gertsch (Stemonyphantinae). The pimoids (which contain 21 species, including 11 new species (Hormiga, in press) are represented here by five species: *Pimoa* (=*Louisfagea*) *rupicola* (Simon), *P.* (=*Louisfagea*) *crispa* (Fage), *P. altioculata* (Keyserling), *P. breviata* Chamberlin and Ivie, and *P. curvata* Chamberlin and Ivie. *Tetragnatha versicolor* Walckenaer and *Zygiella x-notata* (Clerck) are used as outgroups of the pimoid-linyphiid clade. The affinities of *Zygiella* are problematic: the genus is currently placed in Tetragnathidae, although not long ago it was thought to belong in Araneidae. Recent analyses of Araneoidea relationships by Coddington and Scharff suggest that *Zygiella* is either sister to Araneidae or Araneinae, i.e. it is the most basal taxon within araneids or basal within the araneine clade (Scharff and Coddington, pers. comm.).

Taxonomic note: I have used taxonomic decisions that will be soon discussed in greater detail elsewhere. The Pimoinae Wunderlich are raised to familial status (Pimoidae, NEW RANK) and are therefore removed from the Linyphiidae. Treating pimoids as a linyphiid subfamily produces a great change in the diagnosis of Linyphiidae, since it is largely based in male genitalic characters which are absent in the Pimoidae (e.g., intersegmental paracymbium, loss of the araneoid conductor, loss of the araneoid median apophysis, presence of a radix and a column, etc.). Once it is established that pimoids and linyphiids are sister-groups, the assignment of ranks is arbitrary. The exclusion of pimoids renders Linyphiidae more homogeneous and easier to diagnose. *Louisfagea* Brignoli, as presently defined, is polyphyletic (Hormiga, in press). The removal of *crispa* would leave the remaining species of *Louisfagea* as a paraphyletic genus. *Louisfagea* is regarded here as a junior synonym of *Pimoa* Chamberlin and Ivie (NEW SYNONYMY). Throughout this paper the taxon name Linyphiidae (linyphiids) does not include the pimoids.

Characters

The data set contains 47 characters (Table 1): 33 male and female genitalic characters, 5 spinneret spigot characters, 7 other morphological somatic characters, and 2 behavioral characters. The data consist mostly of original observations, but a few characters have been extracted from the literature. Although this data set integrates information from several character systems, it especially focuses on male palp and spinneret spigot morphology. The methods of study and of homology assessment of spinneret spigot morphology follow those of Coddington (1989). The work on linyphiid morphology (including the descriptive studies on male palp, spinneret spigot, and tracheal system morphology) will also be published elsewhere.

Analysis

The data set was analyzed using the computer program for phylogenetic analysis Hennig86 ver. 1.5 (Farris, 1988). Multistate characters were treated as non-additive (unordered).

RESULTS

Characters

Character distributions are summarized in Table 1. The desmitracheate tracheal system (*sensu* Millidge, 1984; character 35) is a synapomorphy of the erigonine clade. I have not been able to confirm some of the tracheal morphologies described by Millidge (1986). I have examined the tracheal system of several erigonine genera (*Erigone aletris* Crosby and Bishop, *E. psychrophila*, *Gonatium rubens* (Blackwall), *Grammonota angusta* Dondale, and *Hypselistes florens* (O.P.-Cambridge)) and have not found evidence of the median tracheae open-

TABLE 1. Rows represent characters and columns taxa. The first state is 'state 0', the second is 'state 1', etc. '?' represents missing data, and '—' non-applicable states. The last two columns give the consistency index (CI) and the weight (W) assigned to the character in the successive character weighting analysis (see text). Taxon numbers: 0 = *Tetragnatha versicolor*, 1 = *Zygiella x-notata*, 2 = *Linyphia triangularis*, 3 = *Microlinyphia dana*, 4 = *Bolyphantes luteolus*, 5 = *Lepthyphantes tenuis*, 6 = *Erigone psychrophila*, 7 = *Walckenaeria directa*, 8 = *Haplinis diloris*, 9 = *Novafroneta vulgaris*, 10 = *Stemonyphantes blauveltae*. The remaining taxa are species of *Pimoa*: 11 = *rupicola*, 12 = *crispa*, 13 = *altioculata*, 14 = *breviata*, 15 = *curvata*. Characters: 1-30, male genitalia; 31-33, female genitalia; 34-40, somatic morphology; 41-45, spinneret spigot morphology; 46, 47, behaviour.

		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	CI	W
1	Cymbium morphology: without dorsoectal denticulated process (DDP); with DDP	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1.00	10
2	DDP denticles: numerous (20); few (<20)	—	—	—	—	—	—	—	—	—	—	—	0	0	1	1	1	1.00	10
3	Pimoid cymbial sclerite (PCS): absent; present	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1.00	10
4	PCS -cymbium connection: sclerotized, rigid; membranous, flexible	—	—	—	—	—	—	—	—	—	—	—	0	1	1	1	1	1.00	10
5	PCS membranous ridge: absent; present	—	—	—	—	—	—	—	—	—	—	—	1	0	0	0	0	1.00	10
6	PCS shape: U; elongated anteroposteriorly; reversed J	—	—	—	—	—	—	—	—	—	—	—	0	2	1	1	1	1.00	10
7	Paracymbium attachment:integral; intersegmental	1	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0.50	4
8	Paracymbium morphology: straight; large-pointed apex; U or J; linguiform-fused to PCS; triangular; short-procurved; *St* type	0	1	3	3	3	3	3	3	3	3	2	4	6	5	5	5	1.00	10
9	Paracymbium apophyses: present; absent	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	0.50	3
10	Petiole:otherwise; fused to subtegulum	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	10
11	Tegular suture: conspicuous; subtle or absent	—	—	—	—	—	—	—	—	—	—	—	0	0	1	1	1	1.00	10
12	Mynoglenine tegular apophysis: absent; present	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1.00	10
13	Suprategulum: absent; fused; articulated	0	0	1	1	1	1	1	1	0	0	2	0	0	0	0	0	1.00	10
14	Median apophysis: present; absent	1	0	1	1	1	1	1	1	1	1	1	0	0	0	1	1	0.33	3
15	Conductor: present; absent	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1.00	10
16	Conductor form: small and undivided; large and bilobate	0	0	—	—	—	—	—	—	—	—	—	0	0	0	1	1	1.00	10
17	Embolus length: long and filiform; short	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0.50	2
18	Embolic membrane: absent; present	—	0	1	0	1	1	1	1	1	1	0	—	—	—	—	—	0.50	2
19	Pimoid embolic process (PEP): absent; present	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1.00	10
20	PEP conformation: undivided; divided	—	—	—	—	—	—	—	—	—	—	—	1	0	0	0	0	1.00	10
21	PEP base: narrow; wide and lamelliform	—	—	—	—	—	—	—	—	—	—	—	0	0	1	1	1	1.00	10
22	Radix: absent; present	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0.50	4
23	Column (distal haematodocha): absent; present	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0.50	4
24	Fickert's gland: absent; present	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1.00	10
25	Terminal apophysis: absent; present	—	0	1	1	1	1	1	0	0	0	0	—	—	—	—	—	0.50	3
26	Lamella characteristica: absent; present	—	0	1	1	1	1	0	0	0	0	0	—	—	—	—	—	1.00	10
27	♂ pedipalpal tibial apophysis: absent; dorsal, rounded; retrolateral; ventral	0	0	0	0	0	0	2	2	0	0	3	1	1	1	1	1	1.00	10
28	♂ pedipalp tibial spines: not clustered; distal row	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1.00	10
29	Prolateral trichobothria in male palpal tibia: two; one	0	0	1	1	1	1	1	1	0	1	1	0	0	0	0	0	0.50	4
30	Retrolateral trichobothria in ♂ palpal tibia: 2; 4; 3:>4	1	0	2	0	0	0	0	0	2	0	0	2	2	2	2	2	0.50	3
31	Epigynum form protrudes: less than its width; more	—	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1.00	10
32	Dorsal plate of epigynum, projections: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1.00	10
33	Atrium: absent; present	—	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0.50	2
34	Mynoglenine cephalic sulci: absent; present	0	0	0	0	0	0	?	0	1	1	0	0	0	0	0	0	1.00	10
35	Tracheal system: haplotracheate; desmitracheate	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1.00	10
36	Ectal chelicerae of ♂: smooth; with stridulatory striae	0	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	0.33	1
37	Retrolateral teeth ♀ chelicera: 3; >3; 2	0	0	1	1	1	1	1	0	1	1	?	2	0	?	2	2	0.50	5
38	♀ pedipalpal tarsal claw: present; absent	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0.50	2
39	Leg autospasy: otherwise; at patella-tibia	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	10
40	Trichobothrium metatarsus IV: present; absent	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0.50	3
41	PMS: with anterior aciniform brush; without	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	10
42	Aciniform spigots in ♀ PMS: > 1; 1; absent	0	0	0	0	0	0	0	0	0	0	2	2	1	2	2	2	0.66	10
43	PLS mesal cylindrical spigot base: same size; enlarged	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	10
44	PLS aciniform field: random spigots; elongated field	1	0	1	1	1	1	1	1	1	1	1	—	—	—	—	—	1.00	10
45	Aciniform spigots in ♀ PLS: >1; 1; absent	0	0	0	0	0	0	0	0	0	0	2	1	1	2	2	2	0.66	10
46	♂ spins sperm web while: above sperm web; below it	?	?	0	0	?	0	1	?	1	?	?	?	?	?	?	?	1.00	10
47	♂ position during ejaculation: above sperm web; below	?	?	0	0	?	0	1	?	1	?	?	?	?	?	?	?	1.00	10

ing directly to separate spiracles, as Millidge reported. The mentioned erigonines posses a tracheal atrium (*contra* Millidge, 1986:57), which, using an aqueous solution of chlorazol black, stains similarly to the rest of the tracheal system. The spiracle is most visible at both ends, where it is wider and rounded, although there is a slit connecting both ends. Such ends are not a closed circle (i.e., they are not separate spiracles), as Millidge's illustrations seem to suggest (e.g. his figure 5), since they are open at its inner part to the interconnecting slit. *Stemonyphantes blauveltae* and *Allomengea pinnata* (Emerton) have tracheal atria opening through a single spiracle, contrary to Millidge's assertion that in both genera the atrium opens via two spiracles. Atria opening via a single spiracle were also found in *Drapetisca alteranda* Chamberlin, *Centromerus sylvaticus* (Blackwall), *Lepthyphantes flavipes* (Blackwall), *L. tenuis* (Blackwall), and *L. intricatus* (Emerton). These latter genera were also reported by Millidge (the first one only implicitly) to have the atrium opening via two spiracles. In the two latter species the slit is very similar to the one reported here for the erigonines, with markedly wider round ends (this fact might have caused them to be taken as having two spiracles).

The spinneret spigot morphology characters (41-45) support the monophyly of the pimoids and of the pimoid-linyphiid clade (Hormiga, in press). Linyphiid and pimoid spigot morphology is consistent with the araneoid groundplan (Coddington, 1990b; Peters and Kovoor, 1991; Hormiga, in press). The pimoid-linyphiid clade lacks the PMS aciniform brush found in primitive orbicularians (character 41), but so do many tetragnathids and the theridiids. Pimoids and linyphiids share the position of the mesal cylindrical spigot on the periphery of the PLS, but this is not exclusive to the pimoid-linyphiid clade: it is also found in *Zygiella x-notata* (pers. observ.) and in some other tetragnathids (Coddington, pers. comm.; Platnick *et al.*, 1990). An enlargement of the base of the peripheral cylindrical spigot of the PLS (character 43) is characteristic of pimoids and linyphiids. Pimoids have drastically reduced the PMS and PLS aciniform fields (characters 42 and 45): they either have one or none aciniform spigots on each spinneret. *Stemonyphantes* has also lost, presumably in parallel, the aciniform spigots in both the PMS and the PLS.

The use of the mating sequence and the transfer of sperm (characters 46-47) as taxonomic characters in linyphiids was studied by van Helsdingen (1965, 1969, 1983). Blest and Pomeroy (1978) studied the sexual behavior of *Haplinis diloris*. I have used data from van Helsdingen's observations as valid for the different species of *Lepthyphantes* and *Microlinyphia* in my data, under the assumption that there is no variation for the characters under study at the intrageneric level. For *Erigone psychrophila*, I have also used data from other species in the same genus, namely *E. dentipalpis* and *E. longipalpis* (Gerhardt (1927, 1923) cited in van Helsdingen (1983)). The male position during the construction of the sperm web (fork and web) and during ejaculation is below the sperm web in erigonines and mynoglenines, and above (only the web, the fork is constructed from below) in Linyphiini and Micronetini.

Analysis

The data (Table 1) were analyzed using the implicit enumeration option of Hennig86, which found four equally parsimonious cladograms with a length of 81 steps and consistency and retention indices of 0.74 and 0.81 respectively. These four topologies differ in the interrelationships of pimoids and in the position of *Stemonyphantes*, which in one of the four cladograms is sister to the pimoids. This latter topology is the result of the parallel loss of the aciniform fields in pimoids and linyphiids. Deactivating the characters that account for the number of aciniform spigots in the PMS and PLS (42 and 45, respectively) and using the implicit enumeration option three cladograms are obtained. These three cladograms are the same as those obtained with the 'active' characters, with the exclusion of the topology that clusters *Stemonyphantes* with pimoids. Successive character weighting (Farris, 1969; Carpenter, 1988) was used, as implemented by Hennig86, to choose a cladogram from the set of four equally parsimonious cladograms. A single iteration produced one cladogram (Fig. 1), which corresponds to one of the original set of four. This result is stable in a second iteration. Because this cladogram is based on the most consistent characters it is preferred as a hypothesis for explaining the relationships of this sample of taxa. The cladistic analysis of this selection of pimoid taxa produces results (i.e. tree topologies) fully congruent with those obtained in Hormiga (in press), in which a total of 20 pimoid species were analyzed together with the same sample of linyphiids and the two outgroup genera.

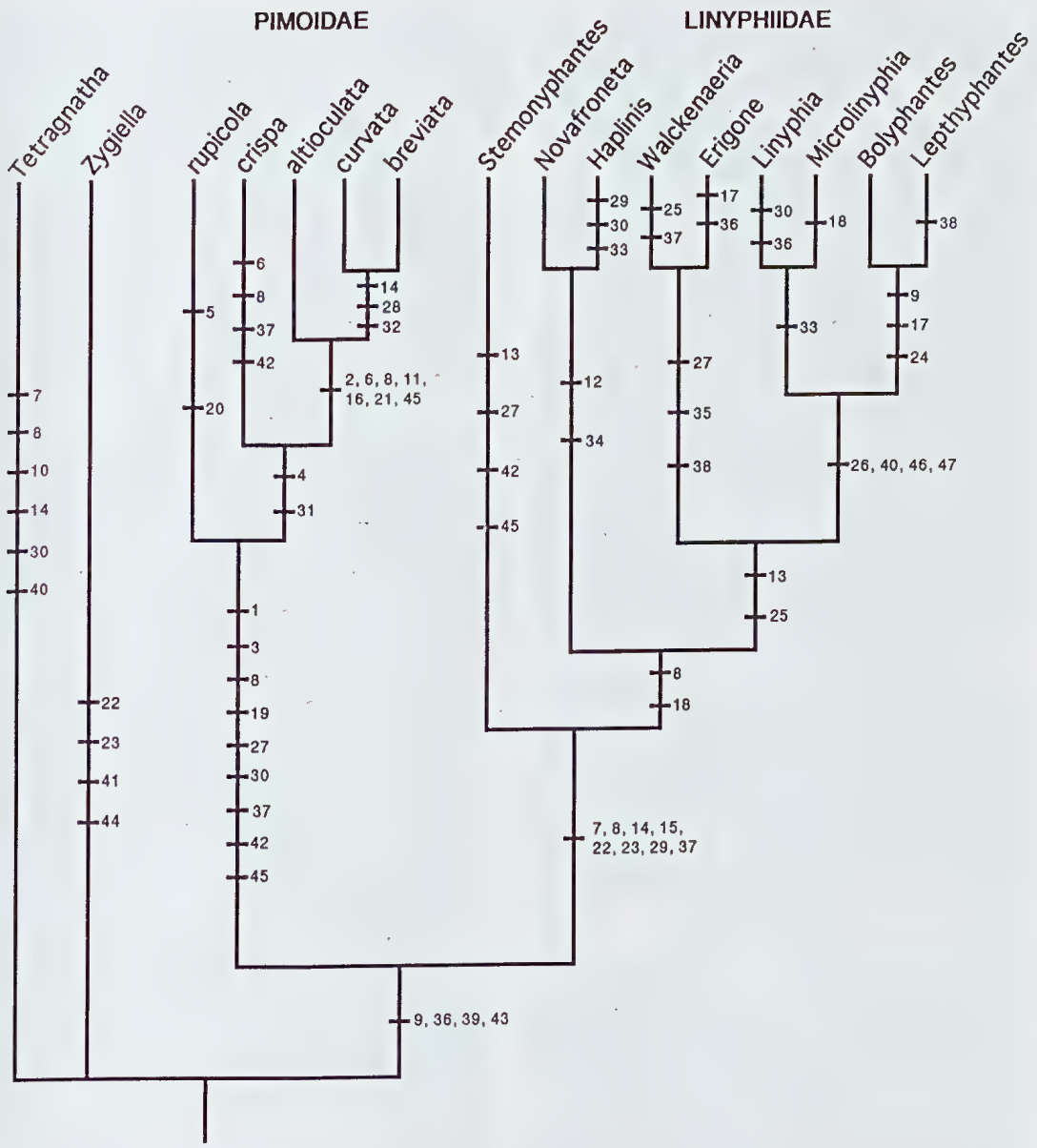

FIG. 1. Preferred minimum length cladogram for the taxa and characters in Table 1 (three equally parsimonious alternative topologies exist; see text). The cladogram length is 81 steps; the consistency and retention indices are 74 and 81, respectively.

DISCUSSION

Monophyly of the Pimoid-Linyphiid Clade

Pimoids and linyphiids emerge as a monophyletic assemblage, unambiguously supported by the presence of cheliceral stridulatory striae, patellar autospasy, and the enlargement of the peripheral cylindrical spigot base in the PLS. Paracymbial apophyses are secondarily absent (i.e. lost) in the pimoid-linyphiid clade, although they are regained in the Micronetini. All these characters (except the patellar autospasy) exhibit some degree of homoplasy.

Millidge (1988) rejected the inclusion of Linyphiidae in Araneoidea, and instead related them to Agelenidae (*s. lat.*), Amphinectidae, and

other taxa currently placed in Amaurobioidea and Dictynoidea. His hypothesis on the exclusion of linyphiids from Araneoidea has been elegantly rebutted by Coddington (1990b), who stated that linyphiids exhibit 9 out of the 10 synapomorphies that support the monophyly of Araneoidea. Pimoids share the same 9 araneoid synapomorphies. Peters and Kovoor (1991) studied the structure, histochemistry, and function of the spinning apparatus of *Linyphia triangularis* and concluded that the data did not provide any indication of close relationship between Linyphiidae and Agelenidae. Certainly Millidge's hypothesis lacks character support. The available data clearly argue in favor of the inclusion of the pimoid-linyphiid clade in Araneoidea. Furthermore, Millidge's idiosyncratic method of phylogenetic inference is flawed because, among other things, it seems to suggest the use of symplesiomorphies (by 'reversing' the outgroup comparison method) to establish family relationships (p. 254). It is well known that grouping by plesiomorphic character states produces paraphyletic groups (Hennig, 1966) and therefore should be avoided.

A major problem in araneoid phylogeny is the placement of the theridiid and the linyphiid-pimoid lineages, in which the orb web architecture has been lost (Coddington and Levi, 1991). Cyatholipidae have been suggested as another possible sister group of linyphiids (Coddington, 1990a). While the sheet web might support this hypothesis, the evidence provided by the morphological data is, at the moment, inconclusive.

Monophyly of Pimoids

Pimoid monophyly is supported by nine synapomorphies, six of them from male palpal morphology and two from spigot morphology. It is interesting to note that none of the pimoid-linyphiid synapomorphies refer to palpal morphology, which is quite different in these two lineages and might reflect a very old time of divergence and/or a rapid rate of character change for the male genitalia. The highly derived spigot morphology of pimoids is unique among araneoids. With the exception of *Stemonyphantes* no other araneoids have been reported to loose all the aciniform gland spigots.

Monophyly, Character Analysis, and Cladistic Structure of Linyphiids

Linyphiid monophyly is supported by eight synapomorphies. Seven of these eight characters (i.e. all except character 8) are homoplasious. With the increasing number of studies that use quantitative cladistic methods it is becoming clear that homoplasy is quite common (Coddington and Levi, 1991). Coddington (1990b) noted that many of the most useful characters for the inference of araneomorph phylogeny were homoplasious. Griswold (in press), in his study of the Lycosoidea, arrived at a similar conclusion for female genitalic characters. Linyphiids are not an exception, and this fact will not surprise most linyphiid taxonomists. For example, intersegmental paracymbia (character 7), similar to the linyphiid type, are also found in *Tetragnatha* and *Pachygnatha* (Levi, 1981:274, 286). Millidge (1988:258) considers the two latter cases as integral paracymbia, different from the linyphiid type, in which case the homoplasy would be removed from this character. But regardless of possible instances of homoplasy, the intersegmental paracymbium is a putative synapomorphy for linyphiids. Coding the paracymbial morphology (character 8) is not an easy task. I have taken a conservative approach by coding it with a high number of character states (seven), in part due to the high morphological diversity of this structure. The coding used produced no extra length (the character's consistency index is 1), but by itself it provides little grouping information (only two states occur in more than one taxon). The states are thus 'ordered' by the tree topology generated by all characters (the final optimization of the character on the cladogram was done by hand, because several equally parsimonious optimizations exist). Blest (1979) and Wunderlich (1986) consider that mynoglenines and erigonines share the same type of paracymbium ('simple paracymbium'). Van Helsdingen (1986:122) argued against this view by pointing out that many linyphiine genera also have the so-called 'simple' paracymbium. Although in some cases erigonines and mynoglenines seem to have morphologically 'simpler' paracymbia (short proximal and distal branches, sometimes J-shaped, without apophyses) than some of the linyphiini and micronetini, I cannot see a clear-cut distinction between these two states. I have coded all the linyphiids (except *Stemonyphantes*) as having the same overall paracymbium morphology (with a proximal and a distal branch of varying length and being more or less J or U-shaped). The paracymbium type found in *Stemonyphantes* is considered by Millidge (1988) as an intermediate form between the integral and intersegmental types. This latter type of paracymbium is inferred to be the primitive state for

linyphiids. This state is subsequently transformed into the paracymbium morphology found in the rest of linyphiids. Coding mynoglenines and erigonines as sharing the same unique character state (i.e., the 'simple' paracymbium), as Blest and Wunderlich have suggested, produces no changes in the cladogram topology.

The presence of a median apophysis and a conductor on the tegulum is regarded as plesiomorphic for araneoids (Coddington, 1990a). Pimoids have a conductor and a median apophysis (Hormiga, in press). The absence in linyphiids of a true (i.e. tegular) conductor and a median apophysis (Coddington, 1990a) are regarded as synapomorphies for linyphiids (characters 15 and 14, respectively). Two potential synapomorphies of linyphiids, the radix and the column, are waiting for resolution of the outgroup of the pimoid-linyphiid clade in order to be tested. The linyphiid radix (character 22) might be homologous to the araneid radix, and therefore plesiomorphic for linyphiids, if araneids are the sister group of pimoid-linyphiids (Coddington, 1990a). The same happens with the linyphiid column or stalk (*sensu* Saaristo, 1971; character 23) that connects the radix to the tegulum/suprategulum. The column could be homologous to the distal haematodocha if araneids are sister to the pimoid-linyphiid clade (Coddington, 1990a). If that is not the case, the homology of the linyphiid radix and column with its presumed equivalents in Araneidae might be refuted, and these characters would function as synapomorphies of linyphiids (this latter alternative is the one mapped on Figure 1). Linyphiids seem to have reduced the number of prolateral trichobothria in the male palpal tibia (character 29) from two (pimoids and outgroups in the data set) to one. However this putative synapomorphy of linyphiids might loose generality (i.e. might be refuted) in a data set with a larger sample of taxa. The same might happen to the number of retrolateral teeth on the female chelicera (character 37), which is four or more in all but one of the linyphiid taxa in the data set, and acts as putative synapomorphy for linyphiids.

The linyphiid suprategulum (character 13) is a projection of the tegulum that bears the column and through which the sperm duct passes (Saaristo (1971, 1975); Millidge (1977); Coddington (1990a)). However, the suprategulum might not be homologous across all linyphiids. The tegular projection that Blest (1979, figs 596-602) and Blest and Pomeroy (1978, figs 2, 4) call the 'suprategulum' in New Zealand mynoglenines does not bear the column (which in some cases is far from it, e.g. *Pseudafroneta*, in Blest's figure 597) and has no sperm duct going through it. I have interpreted the mynoglenines as lacking a suprategulum (*sensu* Saaristo) and coded its tegular apophysis as a structure synapomorphic for mynoglenines and not homologous to the suprategulum ('mynoglenine tegular apophysis', character 12). However, the tegular apophysis of *Haplinis* seems to be functionally analogous to the suprategulum in some linyphiids (van Helsdingen (1965, 1969); Blest and Pomeroy (1978)) in engaging the socket of the epigynal scape, but data on the functioning of the genitalia across taxa are still very scarce. The suprategulum of *Stemonyphantes* is articulated to the tegulum by means of a membranous connection (van Helsdingen, 1968:124; pers. observ.) and is different from the rest of linyphiid suprategula which are fused to the tegulum (character 13). The cladogram in Figure 1 suggests the possibility of independent origins for these two types of suprategula, and therefore questions its homology (secondary absence of the suprategulum in the mynoglenines -versus independent gains-requires one additional step).

The linyphiid embolic membrane (van Helsdingen, 1969) is not homologous to the araneoid conductor because of their different position (but see Coddington, 1990a:16). The embolic membrane (character 18) is a putative synapomorphy for all linyphiids, with the exclusion of the basal genus *Stemonyphantes*. The 'embolic membrane' *Microlinyphia* is not an outgrowth of the column, as in most linyphiids (van Helsdingen, 1986:123), but a structure 'arising from (the) membranous connection of radix, base of embolus, and dorsal side of lamella' (van Helsdingen, 1970:6). I have interpreted it as not homologous to the column-positioned embolic membranes, but the nature of this membrane remains dubious. The alternative, i.e. coding it as an embolic membrane shifted to a radical position in *Microlinyphia*, produces no change in the cladogram topology.

The terminal apophysis (character 25) is a synapomorphy for erigonines plus linyphiines, but its interpretation offers several problems. The first is its homology with its homonym in araneids (Saaristo 1971, 1975; Coddington, 1990a). Such homology is dependent, among other things, on a sister-group relationship between araneids and linyphiids (plus pimoids), but even so the homology is not obvious. *Zygiella x-notata* (which is considered here as an araneid) lacks anything

similar to a terminal apophysis, pimoids lack the radix (therefore, we do not know if they ever had such apophysis), and basal linyphiids (i.e. *Stemonyphantes* and the mynoglenines) have simple radices and no terminal apophysis. The cladogram in Fig. 1 suggests independent origins (i.e. non homology) for the terminal apophysis in araneids and linyphiids. If the embolic division of *Stemonyphantes* is interpreted as simple (and not simplified) it also suggests that complex embolic divisions in araneids and in linyphiids arose independently. This latter interpretation would question the monophyly of araneids plus linyphiids (e.g. Coddington, 1990a:14). Second, and at a less inclusive level, not all erigonines and linyphiines have a terminal apophysis. Evaluation of the homology of these apophyses requires a more detailed cladistic structure for the family (i.e. more taxa and more characters). Another radical sclerite, the lamella characteristica (character 26), is a putative synapomorphy for the linyphiines. Further support for the monophyly of Micronetini plus Linyphiini is given by the loss of metatarsus IV trichobothrium (character 40) and the position of the male during the construction of the sperm web and during ejaculation (characters 46 and 47). The phylogenetic information provided by the latter two characters should be regarded as provisional, because of the high number of missing entries for these characters in the matrix. According to Blest and Pomeroy (1978) *Haplinis* is unique among linyphiids in having an expansion of the palp prior to its locking to the female genitalia, while in the remaining linyphiids for which this trait is known the male first locks its palp to the epigynum and then expands the haematodocha. However, in a recent study on African linyphiids Scharff (1990:62) described a similar expansion prior to locking for *Neriene kibonotensis* (Tullgren). More data on the distribution of this character are needed in order to establish it as a mynoglenine synapomorphy.

Erigonine monophyly is supported by the retrolateral tibial apophysis of the male palp, the loss of the female palpal claw, and the desmitracheate tracheal system (*sensu* Millidge, 1984). In the present dataset the epigynal atrium (character 33) is the only synapomorphy supporting the monophyly of Linyphiini. An epigynal atrium is also present in the mynoglenine genus *Haplinis* (Blest, 1979:100) but absent in *Novafroneta* (Millidge 1984:241). The cladogram suggests independent origins for these two atria; its homology is therefore questionable (similar epigynal atria are also present in other linyphiids, not included here, that are not closely related to the Linyphiini; Millidge, 1984; van Helsdingen, *in litt.*). Three synapomorphies support the monophyly of Micronetini: the paracymbial apophyses, a short embolus (it also occurs in *Erigone*), and the presence of Fickert's gland in the radix.

The nature of the clypeal glands is another interesting problem in linyphiid evolution. Whether the mynoglenine sub-ocular sulci are or are not homologous to the male erigonine post-ocular sulci is a matter of debate. Mynoglenine sub-ocular sulci are found both in males and females (they are very similar in both sexes; juveniles also have functional sulci, at least in the species of *Haplinis* studied by Blest and Taylor, 1977), they do not play any active role during the courtship (at least in the species studied by Blest and Pomeroy, 1978), and they probably elaborate defensive secretions (Blest and Taylor, 1977; but this latter hypothesis has not been empirically tested, although the unique ultrastructure of the clypeal secretory cells is consistent with the synthesis of a toxic product). On the other hand, erigonine post-ocular sulci (as well as the cephalic elevations) are found (mostly) in adult males. These erigonine sulci usually have pores associated with glands that are cytologically different from those of the mynoglenine sulci (Blest and Taylor, 1977; Schaible *et al.*, 1986; Schaible and Gack, 1987), and they play an active mechanical role during the courtship (they are gripped by the female cheliceral fangs). Nevertheless, these erigonine glands are not always associated with cephalic specializations. Mynoglenine and erigonine ocular sulci can be interpreted as homologous structures within the same transformation series or as two independent developments. The available evidence is not easily interpreted in either way. The mynoglenine and erigonine sulci differ in their position, in the cytological structure of their associated glands, and in their behavioral role. It seems that the available data argue against the homology hypothesis, since they fail to meet the classical homology criteria of position and detailed similarity. Congruence with other character systems offers a powerful test of the homology hypothesis of the sulci. Blest (1979:165) argued that the most economical hypothesis (i.e. parsimonious) 'would suggest that the sulci of the mynoglenine type gave rise directly to the kind found in Erigoninae'. Mapping his hypothesis on his cladogram (*op. cit.*, p. 172, which in parenthi-

cal notation can be summarized as: Mynogleninae (Linyphiinae, Erigoninae)) requires the gain of the mynoglenine type of sulci in the common ancestor of all linyphiids, profound modifications (morphological, cytological, and behavioral) of the sulci to achieve the erigonine type of sulci (either in the ancestral erigonines or at the level of the linyphiine-erigonine ancestor) and finally the loss of the sulci (and its accompanying glands and behavior) in the linyphiines. The alternative hypothesis (i.e. non homology of mynoglenine and erigonine sulci) maps on the mentioned cladogram as two independent gains of the two types of sulci. The evolution in parallel of the erigonine and mynoglenine sulci would then account for their differences. Although the latter hypothesis is more parsimonious (in both Blest's and my cladogram) this question cannot be truly tested until more data (taxa, particularly those with any type of sulci and/or glands, and information on the glands) are included in the data set. This is due to the effect that mynoglenine and erigonine cladogram topologies might have on the optimization of the character(s) on the linyphiid cladogram. Only then we will be able to asses alternative hypotheses on the evolution of these cephalothoracic specializations.

The linyphiid tracheal system needs to be studied in detail and re-evaluated. New morphological descriptions are needed, since at least some of the available comparative data are inaccurate (see above). Millidge's (1986, figure 12) scheme for the evolution of the tracheal system in linyphiids is therefore not valid, because it is partially based on inaccurate data.

The most parsimonious hypothesis to explain the data presented in this study is the cladogram depicted in Figure 1, which suggests (as well as the three equally parsimonious alternatives that exist) relationships different from those proposed by Wunderlich (1986:106). The mynoglenines are considered here to be relatively basal linyphiids, while Wunderlich suggested them as sister to the erigonines. Both hypotheses agree on considering the pimoids and *Stemonyphantes* as the most basal clades, and on the monophyly of the Micronetini plus the Linyphiini. To use either of these two phylogenies as a classification would be premature. Wunderlich did not explicitly list the synapomorphies that define the monophyletic groups in his cladogram, synapomorphies are mixed up with diagnostic characters (some of which are not synapomorphic), and there is no mention of the genera included in each monophyletic group, even in a schematic manner. My study should be considered only a preliminary sketch of linyphiid relationships. Clearly, a much larger sample of taxa is needed before the main monophyletic groups can be established. The addition of new taxa and new characters might affect the cladogram topology presented here. As we have seen, non-homoplasious characters for wide ranges of taxa are more the exception than the rule, and different character systems often delimit conflicting monophyletic groups. When large numbers of taxa and characters are studied quantitative studies are imperative. Cladistic studies provide explicit and testable hypotheses of relationship and are recognized as the most reliable method for retrieving the phylogenetic pattern that underlies organic diversity. Not until this approach is adopted will advances in linyphiid higher classification become a reality.

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CRITERIA FOR IDENTIFYING THERMAL BEHAVIOUR IN SPIDERS: A LOW TECHNOLOGY APPROACH

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The widespread occurrence of thermal behaviour in diurnally active web spiders is either largely ignored or not recognised. Thus it obfuscates some explanations of the function of the stabilimentum on spiders webs. Thermal behaviours of four spiders (*Nephila edulis*, *N. maculata*, *Gasteracantha minax* and *Neogea* sp.) are examined using technology which is often inappropriate for field studies. Many thermal behaviours are recognised as well as behaviours which facilitate thermal behaviour. The thermal correlates of these behaviours are established. Some observational criteria are derived, which require only simple equipment, by which thermal behaviours may be recognised in the field and distinguished from other behavioural patterns.□*Araneae, orb-weavers, thermal behaviour, thermoregulation, stabilimentum.*

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Many orb-web spiders remain active at the web hub during the day, where they can continue to feed, mate, and defend their web site from the same and other species, as well as produce or respond to attractant signals (acoustic, tactile, visual or chemical). The seasonal and diurnal duration of this activity can be extended by adopting behaviours that warm the spider (Robinson and Robinson, 1974, 1978; Biere and Uetz, 1981) when it would otherwise be too cold or else that prevent it from overheating (Lubin and Henschel, 1990; Humphreys, 1978, 1987a, 1991, 1992).

I consider below mainly behaviours that prevent overheating. In essence, in hot weather the spider postures so as to align the long axis of its body with the sun's rays and in this position it tracks the sun's apparent movement during the day. Such behaviour is not exclusive to spiders of open country nor in tropical climates but is found also in both temperate and tropical forest spiders (Biere and Uetz, 1981; Humphreys, 1991, 1992 and unpublished). The standard interpretation of this thermal behaviour relies on a simple physical model; posturing minimises the projected surface area (silhouette) exposed to the sun's radiation and so reduces the heat load (Fig. 1), lowering equilibrium body temperature (Willmer and Unwin, 1981: but see Humphreys, 1986) or, in an anti-predator hypothesis, minimising the silhouette against the brightest background, else the body area most brightly illuminated.

Recent observations have shed some light on this seemingly simple process and revealed a sequence of behaviours serving to reduce progressively the heat loading, behaviours that are themselves mostly graded (Humphreys, 1992). These include stilting, drooping, orientation, front leg raising, abdomen pointing, posturing, front leg rotation and web abandonment. Associated behaviours include silk laying and agitation (Humphreys, 1992 and unpublished). In addition, the use of a disc stabilimentum as a sun shade, suggested by Robinson and Robinson (1973: 283), is an effective thermal behaviour in *Neogea* sp. (Humphreys, 1992). Such behaviours not only maintain the animal within its heat tolerance range, but also serve to maintain the body temperature (T_b) within a narrow range (presumably some optimum temperature) for extended periods of time (Humphreys, 1974, 1978, 1991). As body temperature has wide implications in physiological, behavioural, ecological and evolutionary contexts (Willmer, 1991), it is important to recognise thermal behaviour in spiders in order to allow different types of explanations for their behaviours.

That the thermal behaviour of spiders is not being recognised or is not being reported in the literature can be drawn from work on stabilimenta on spiders' webs. While stabilimenta have many different forms, they are mostly thought to provide mechanical support (Robinson and Robinson, 1973), to function as anti-predator devices (Eberhard, 1973, Edmunds and Edmunds, 1986; Lubin, 1986), to attract prey (Ewer, 1972; Craig and Bernard, 1990) or to collect water (Olive, 1980; see also Ewer, 1972; Robinson and Robinson, 1973: 283). *Neogea* sp. in

Papua New Guinea uses a disc stabilimentum as a parasol, which, together with a sequence of other behaviours, each themselves graded, reduces its heat loading (Humphreys, 1992). The demonstration that stabilimenta may be used in a thermoregulatory role raises questions concerning many observations which have been interpreted as supporting the anti-predator role of stabilimenta.

Some observations and deductions have resulted in an anti-predator function being ascribed to the stabilimentum. However, in the absence of other information, these observations are equally open to interpretation in terms of thermoregulatory hypotheses (see Humphreys, 1992). For example -1. Only spiders that remain at the hub of the web during the day produce stabilimenta (Eberhard, 1973). 2. Spiders with stabilimenta may shuttle from one side of the web to the other (*ibid.*). 3. The legs assume an 'aligned posture' by day but not by night (*ibid.*). 4. The amount of silk used is directly related to openness of the habitat (Marson, 1947).

Eberhard (1973) found that *Uloborus diversus* Marx used more silk in its stabilimentum on light than on dark nights (see also 4. above). The trend for larger stabilimentum at brighter sites camouflaged those spiders most susceptible to attack. However, without pertinent behavioural data, it is not possible to refute the hypothesis that the open sites are more exposed to direct sunlight and thus that the stabilimenta are used to protect the spider from ultra violet light (but see Craig and Bernard, 1990) or to reduce its heat load.

Posturing by spiders that remain by day at the web hub is rarely mentioned in the literature on stabilimenta and defense mechanisms. For example, although Edmunds and Edmunds (1986: 83) found that species of *Argiope*, *Nephila*, *Leucauge*, *Cyrtophora* and the Gasteracanthinae remain at the hub of the web during the day, they made no mention of posturing. In the Australasian region species in all these genera readily posture and track the sun (Humphreys, 1991, 1992; W.F. Humphreys, unpublished).

Clearly, thermoregulation hypotheses need more consideration in field studies of diurnally active spiders. More recently this has occurred (Henschel *et al.*, 1992; Humphreys, 1991, 1992; Lubin and Henschel, 1990; Ward and Henschel, 1992) but such studies often require expensive equipment to examine the thermal behaviour. Such equipment may be inappropriate to a field biologist primarily interested in observation and manipulation to examine behavioural or sociobiological problems. There needs to be some observational criteria using only low technology by which thermal behaviour may be recognised and distinguished from other behavioural patterns.

The examination of thermoregulation in orb-weaving spiders is problematical as most methods used on vagrant spiders (thermal preferendum apparatus, thermocouple implantation, temperature transmitters) are not appropriate. The most promising apparatus for such studies is the use of remote infrared telemetry (Suter, 1981; Humphreys, 1991, 1992), although model spiders may be effectively used to determine T_e (Riechert and Tracy, 1975; Henschel *et al.*, 1992).

Can criteria be established which would enable workers, using cheap and readily available equipment, to establish that spiders are behaving in a manner consistent with thermoregulation and to identify the thermal conditions under which they initiate such behaviour?

METHODS

Observations on *Nephila edulis* (Labillardière) were made both on Rottnest Island and in Perth, on *Gasteracantha minax* Thorell in the south-west, of Western Australia, and on *Nephila maculata* (Fabricius) in mangrove at Port Benoa, Bali, Indonesia.

Spider temperatures were recorded from 1100 -1500 hours using an infra-red thermometer, described elsewhere (Humphreys, 1991, 1992). The temperature was recorded of undisturbed spiders resting above and below the hub of the web, both in the shade and in the sun. It was recorded at intervals and as soon as possible (<3s) after a change in behaviour. Spider behaviour changed according to the incident light; this varied because the site was sometimes shaded by trees or by clouds. To induce more behavioural sequences the spider was sometimes shaded artificially and the direction and strength of the incident sunlight adjusted using a mirror. A plane mirror was used to alter the apparent position of the incident radiation at about the same intensity as the natural sunlight and a concave mirror was used to alter the apparent position of the incident radiation and at an intensity continuously variable from greater to less than the intensity of the direct sunlight. In the field, control of intensity was crude in the wind owing to movement of the web, and hence the spider; control of the intensity

Behaviour	Mean	s.d.	n	Range
Repose in shade	32.6 a	2.10	12	29.0-35.1
Repose in partial sun	32.4 ab	1.59	19	29.2-34.3
Repose in sun	35.0 b	1.66	47	31.6-38.3

TABLE 1. Mean temperature (T_b °C) of *N. edulis* in Repose position on Rottnest Island, Western Australia. T_b of spiders in Repose differs according to energy intensities of their location (shaded, partly shaded, sunlight: ANOVA - $F_{S\ 2,75} = 19.895$, $P<0.001$). Common letters include means not differing significantly (Fisher's PLSD at $\alpha= 0.05$).

of radiant energy is therefore relative and greater or less than the natural incident radiation.

The following temperatures are mentioned: T_a = of ambient shaded air; T_b = of the spider 's body which by default is the abdomen (T_{ab}), otherwise the thorax (T_{th}). The environmental temperature (T_e) which is used as a shorthand for the effective heat load on the spider taking account of all energy gains and losses. Means are followed in parentheses by the standard deviation of the mean, and sample size.

Definitions required for this discussion are given below (see also Humphreys, 1991, 1992).

Abandon web: the spider leaves the web, often after a sequence of very agitated movements, and moves to the shade provided by the objects to which the main anchor lines of the web are attached.

Abdomen pointing: the abdomen alone is orientated to the sun as a prelude to full posturing. This behaviour is strongly represented in some species (Humphreys, 1992).

Agitation and body lift: the spider appears agitated and circles its body around the web's hub and in the process the body is raised away from the web. The latter is sometimes seen on its own and they are included here under the same behaviour. This body lift is not comparable to stilting (Humphreys, 1992).

Drooping: the spider hangs limply from the back legs with apparent loss of hydrostatic pressure; the appearance is like that adopted by a spider immediately after moulting while the new cuticle is hardening.

Fabian position (Humphreys, 1991): the spider aligns its long axis parallel to the direction of incident sunlight with the prosoma facing away from the sun. This position may be achieved by orientation and/or posturing. When the incident sunlight is parallel to the web plane then the Fabian position may be the same as the Repose position (Humphreys, 1991). Continued adoption of the Fabian position results in the long axis of the spider tracking the sun during the day.

Front legs raised: legs I and II are raised off the web and aligned parallel to the incident radiation; this occurs as a graded sequence with the first pair being raised before the second pair.

Orientation: the angle of the saggital plane of the spider is rotated to lie parallel to the solar azimuth while the long axis of the body stays in the plane of the web.

Part orientation: the spider is not in the Repose position and has partly orientated its saggital plane between the Repose position and the orientated position.

Posturing: change in the angle between the web plane and the anterior-posterior axis of the spider.

Repose position: spiders occupy the lower or upper surface of the hub with the prosoma pointing downwards; the anterior-posterior axis of the spider is parallel to the plane of the web.

Rotate front legs: following front legs raising the legs are rotated forwards such that they are stretched out in front of the spider and lie in the shade of its body when it is fully postured; this may occur as a graded sequence with the first pair being rotated before the second pair.

Silk laying: adjusts the web stuctrure near the hub apparently to aid leg placement the better to posture and orientate to achieve the full Fabian position. This facilitates subsequent thermoregulatory behaviour but is not itself thermoregulatory.

Start to posture: when the spider changes the angle between its anterior-posterior axis and the plane of the web such that its long axis is parallel to the incident radiation.

Stilting: describes the 'standing on tiptoe' behaviour of scorpions used to prevent overheating (Alexander and Ewer, 1958); here it describes similar behaviour in spiders (Humphreys, 1992).

EVIDENCE

Statements otherwise unsupported are based on my unpublished observations.

Repose Position And Thermoregulation

Spiders adopt the repose position if T_e is below some critical level and they do so whether they are in shade or sun, hence, direct sunlight alone does not cause spiders to posture. However, T_b in sun is higher than in shade (Table 1). For example, during cool weather (low T_e) in the sun and during hot weather in the shade all individuals are in the Repose position on their webs if not otherwise engaged in activities such as mating, web building, etc.

When T_e is not sufficient to cause posturing in *G. minax* the proportion of spiders in the Repose

position during daylight does not differ between sunlit (36/38) and shaded (32/33) sites (χ^2_1 = 0.016, P= 0.90).

The mean T_b temperature of *N. edulis* in the Repose position was directly related to the intensity of the incident radiation such that spiders in the sun were hotter than partly or fully shaded spiders (Table 1).

Spiders on non-horizontal webs almost invariably rest on the underside of the web with the prosoma pointing down. However, spiders resting in positions other than the Repose position should not be taken as proof of thermoregulatory behaviour because some species, such as *Verrucosa* and *Cyclosa*, reputedly adopt a head up stance (Foelix, 1982: 139), as does *G. minax* at night and *Argyrodes antipodianus* O.P. Cambridge, generally.

Orientation and Posturing: Evidence for Thermoregulatory Function

In hot weather, spiders orient or posture on the web to attain the Fabian position and then track the sun's apparent movement. They do this irrespective of web orientation. Heat and sunlight are needed to obtain these behaviours. On very hot days, spiders may leave the web altogether and seek shade. Large spiders assume Fabian posture earlier than small ones possibly because under given environmental conditions large spiders reach higher body temperatures. However, small spiders may have lower threshold T_b's.

In hot weather an individual spider in the sun will use reorientation and/or posturing to align the anterior-posterior axis of its body parallel to the direction of incident sunlight with the prosoma facing away from the sun and thus achieve the Fabian position (Robinson and Robinson, 1974, 1978; Humphreys, 1991, 1992). The spider will adjust this position during the day and track the apparent movement of the sun (Humphreys, 1991).

In hot weather all individuals in the sun orientate in the same direction irrespective of the orientation of their webs; namely they all assume the Fabian position by posturing and/or reorientation (Humphreys, 1991).

Heat alone does not cause the thermal behaviour because in hot weather under heavily overcast conditions spiders do not assume the Fabian position. However, if intermittent direct sunlight strikes the spider it assumes the Fabian position intermittently.

On very hot days spiders may assume the Fabian position in the morning and afternoon but leave the web to seek shade during the middle of the day. Such activity patterns have been reported for many heliothermal spiders (Humphreys, 1978, 1987a, 1987b) and other taxa (e.g. reptiles: Heatwole, 1970).

N. edulis abandons the web at 44.8°C (±0.50, 3) and moves into shade. In Perth, Western Australia, when the shaded air temperature was extreme (46.2°C) many *N. edulis* failed to seek cooler places and fell dead from their shaded webs through heat stress (G.A. Harold, pers. comm., 1991).

Large spiders assume the Fabian position earlier in the day than do small spiders (e.g., *N. maculata*)–this is consistent with the thermoregulation hypothesis because larger bodies have a higher temperature excess (Willmer and Unwin, 1981). However, the threshold temperatures for given behaviours could be size related and lower in small than in large spiders. This is consistent with the seeming generality that the tolerance zones of animals are related to the temperatures experienced. For example, very small *N. edulis* start to posture at 36.0°C (±2.39, 4), significantly cooler, by an average of 4.4°C ($Fs_{1,25}$ =13.279, p=0.002), than adult spiders undergoing the same behaviour (40.4°C ±2.16, 27).

Orientation and Posturing in Response to Manipulation

Experiments with redirected and intensified sunlight can be conducted to influence the behaviour of spiders to assist in determining whether the behaviour is thermoregulatory without having to measure body temperature. The results are consistent for several species including *Arachnura higginsi*, *N. edulis*, *N. maculata*, *G. minax* and *Neogea* sp.

In cool sunny weather when the spiders are in the Repose position, additional heating (by concentrating redirected sunlight using a concave mirror), results in the spider orientating–and/or posturing if necessary–to assume the Fabian position. The redirected sunlight does not alone alter the behaviour of the spider (sunlight redirected at natural intensity using a plane mirror). Hence, posturing is dependent on the intensity of the heat applied.

In hot weather a spider which has assumed the Fabian position will resume the Repose position if clouds obscure the sun or it is artificially shaded even if lower than the natural insolation is reflected onto it by means of a concave mirror.

Spiders in the Fabian position in the sun will, if artificially shaded, assume a new Fabian position

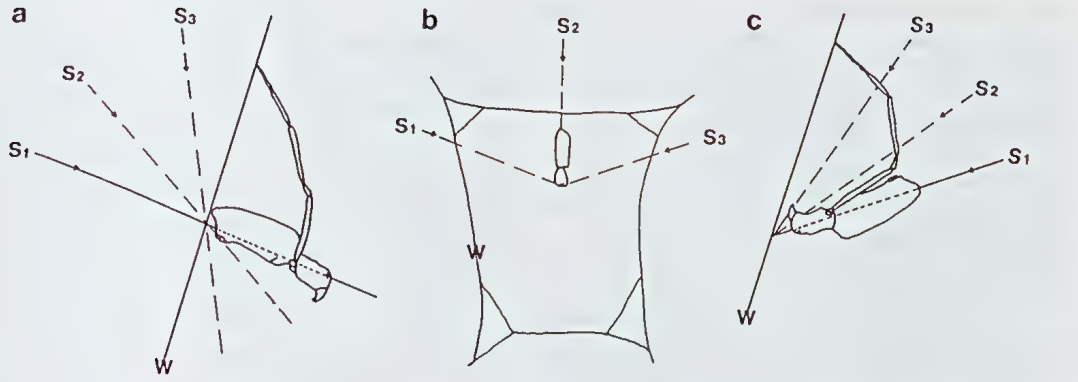

FIG. 1. Thermoregulatory postures adopted by golden web spider, *N. clavipes*. Lines projecting from three successive positions of sun (*S1*, *S2*, *S3*) indicate corresponding orientations of long axis of spider's body. Lateral views (a,c) and plan view (b) of web show posture assumed in response to ventral (through the web) insolation; b lateral insolation; c dorsal insolation (redrawn from Robinson and Robinson, 1974).

if the direction of the sun is artificially changed by means of a mirror.

In hot weather when the spiders are in the Repose position in the shade, redirection of unconcentrated sunlight, by means of a plane mirror or a concave mirror, results in the spider orientating and/or posturing if necessary to assume the Fabian position.

In hot weather, when the spiders are in a Fabian position, adding reflected sunlight from a plane mirror results in the spider orientating with respect to the mean angular direction of the two sources of incident radiation (when angle <90°). A spider posturing between two heat sources will turn towards the one increased in intensity and *vice versa*. Hence, the Fabian position moves towards the incident radiation of the mirror if the heat reflected from the mirror is increased and towards incident radiation of the sun if the heat reflected from the mirror is decreased.

If redirected light comes from above the horizontal plane of the web spiders rapidly change their Fabian position; if redirected light comes from below the horizontal plane of the web, a naturally impossible position, spiders appear confused and change position frequently and some species never achieve the Fabian position (e.g. *N. maculata*).

Cascading Behaviours

Many thermally related behaviours that have been categorised are themselves graded so that they each develop progressively rather than switch from one state to another.

For example as *Neogea* sp. warms in the sun, it exhibits a progression of distinct behaviours, each of which is graded and which are associated with increasing temperature of the abdomen (Humphreys, 1992). When a spider in the Repose position on the disc stabilimentum is heated by the sun it initially 'stilts', as has been described for scorpions. The spider gradually raises its body away from the disc surface until it has full downward extension of all legs and seems to be standing on 'tiptoe', thus removing the body of the spider as far as possible from the disc's surface.

On further heating, *Neogea* sp. progressively orientates its body and then gradually postures, starting with the abdomen. It rotates the tip of the abdomen towards the incident radiation and this minimises the projected surface area of the abdomen exposed to the sun. As the posturing develops the prosoma also is aligned with the abdomen so that the entire spider is orientated prosoma from the sun with minimal silhouette area exposed. Eventually the legs themselves are rotated forwards until they are parallel to the long axis of the spider in which position they are in the shadow of the abdomen, as is the prosoma; this is the full Fabian Position from which the spider tracks the sun (Humphreys, 1991, 1992). By these means the spiders potentially can obtain very fine control of their silhouette area and hence on their temperature.

In *N. edulis* many behaviours were recognisable as similar to those observed in other spiders (e.g. orientation, posturing, agitation: Humphreys, 1991, 1992), whereas others have not previously been reported or recognised (e.g. drooping). Some behaviours recognised may be components of the same behavioural sequence. For example, Agitation, in which the spider circles around the hub, involves the body being raised slightly from the

web, a behaviour sometimes seen on its own. Both behaviours are included here under the same category. Thermally there appears little difference between three categories recognised here as different behaviours (agitation and body lift, front legs raised, and start to posture). Work conducted under more controlled conditions in the laboratory may separate thermally these behaviours or allow their pooling using more rigorous criteria.

Eleven behavioural categories are recognised in *N. edulis*, ranging from Repose to web abandonment which occur between T_b of 33.9 and 44.8°C (Table 2). The spider temperature associated with many of these behaviours is significantly different from others. Some of these behaviours reduce the projected body surface area exposed to the sun and thus, under the predictions of the physical model, should result in lower equilibrium body temperature, all else being equal (e.g. orientation, posturing, leg raising, leg rotation and web abandonment). Other behaviours may not be thermoregulatory but are associated with the onset of the next behaviour in the graded series (e.g. agitation and body lift) or facilitate a subsequent stage (e.g. silk laying to enable correct leg placement for full posturing).

As in *Neogea* sp. (Humphreys, 1992), some behaviours themselves form a graded series which should proffer gradually increased thermoregulatory effects. Both front leg raising and front leg rotation occur initially in the front legs followed by the second pair of legs. In addition contralateral legs are not necessarily lifted or rotated at the same time.

Behaviour	Mean	s.d.	n	Range
Repose - see Table 1	—	—	—	
Part orientation	33.9	0.57	6	33.1-34.7
Drooping	36.5	1.57	8	35.4-38.8
Orientation	38.7a	2.30	9	34.2-40.3
Agitation and body lift	38.7a	2.09	21	35.2-43.5
Front legs raised	38.9a	2.84	11	35.0-43.3
Start to posture	40.4b	2.16	27	34.8-43.6
Silk laying	41.1bc	1.34	6	39.3-42.6
Rotate front legs	42.4cd	0.99	10	41.2-44.3
Abandon web	44.8d	0.50	3	44.3-45.3

TABLE 2. Mean temperature (T_b °C) of *N. edulis* on Rottnest Island, Western Australia, associated with different behaviours (ANOVA - $F_{8,93} = 15.233$, $P<0.001$). Common letters include means not differing significantly (Fisher's PLSD at $\alpha= 0.05$).

DISCUSSION

Two classes of observation refute the hypothesis that posturing serves an anti-predator role as stated in the introduction.

Firstly, if the Fabian position reduce the silhouette area against the brightest part of the sky as an anti-predator defense (i.e. to make them less visible) then they should posture to the sun under clear conditions irrespective of the intensity of the sunlight; they do not. Furthermore, under conditions of patchy heavy clouds (cumulus and cumulo-status) against a clear sky, the spiders should assume a Fabian position with respect to the brightest sector of the sky; they do not.

Secondly, many thermally related behaviours are themselves graded so that they are exhibited progressively as the spider warms. This provides the strongest evidence for the thermoregulation hypothesis because partial stilting, posturing or orientation (Humphreys, 1992) makes no sense under alternative hypotheses but is entirely consistent with, and predicted from, the thermoregulation hypothesis.

The body temperature of a spider is a complex function of many intrinsic factors (size, morphology, attitude, physiology, reflectance, etc.) as well as factors extrinsic to the individual (e.g. wind speed, turbulence, air temperature, incident radiation and its spectral characteristics; Monteith and Unsworth, 1990). It is because T_b is a complex function of intrinsic and extrinsic factors that makes T_a a poor predictor of thermal behaviour. Hence, the observation that a spider may not always assume the Fabian position (or other presumptive thermoregulatory behaviour) at the same T_a does not imply that the behaviour has no thermoregulatory significance. For example, *Lycosa godeffroyi* Koch in Canberra began basking at much lower T_a in winter (4°C) than in summer (17°C) and reached 35°C on clear winter days at T_a of 11°C (Humphreys, 1974, 1978); the latter shows the dominant role of boundary layer effects for such surface dwelling spiders. Although orb-weaving spiders are often high above the ground, such boundary layers may assume more importance in those orb weaving spiders that incorporate a surface in their web (e.g. *Neogea* sp. and leaf curling species; Humphreys, 1992).

These many classes of observation support the hypothesis that the posturing and/or reorientation that spiders undergo in intense sunlight is of thermoregulatory significance. Many are not alone adequate to support unequivocally the thermoregulation hypothesis (e.g. Table 3: 4, 6 , 9), some, in combination with others, support the

Condition at spider	Manipulation	Behavioural response and thermal consequences
1[a] Cool weather in shade	Nil	Repose; $T_b=T_a$
2[a] Cool weather in sun	Nil	Repose; $T_b>T_a$
3[a] Cool weather in sun	$=S$	Repose; $T_b>T_a$
4[a] Cool weather in sun	$>S$	Orientate and/or posture; $T_s>T_e$
5[a] Hot weather in shade	Nil	Repose; $T_b=T_a$
6[a] Hot weather in shade	$=s$ or $>s$	Fabian
7[a] Hot weather in sun	Nil	Orientate and/or postureX tracks sun; minimise T_b
8 Hot weather in sun	$<<S$	Repose
9 Hot weather in sun	$=S$ or $>S$	Fabian
10 Very hot day in shade	Nil	Repose; *in extremis* may suffer heat death without posturing
11 Very hot day in sun	Nil	Seeks shade
12 Population in hot sun	Varied web orientation	All spiders orientate in same direction; minimise T_b
13 Population in hot sun	Large & small spiders	Large spiders posture earlier in day than small
14 Hot weather in sun	$=S$ perpendicular to sun	Spider postures mid-way between two incident heat sources
15* Grade n-1 behaviour	$>S$	Grade n behaviour; behavioural cascade culminating in Fabian
16 Hot weather in sun	$=S$ below horizontal	Apparent confusion in some species;> T_b
17 Cool weather in shade	$=s$	Posture to > exposure to heat source; $T_b>T_a$

TABLE 3. Summary of characteristics of thermoregulatory behaviour in orb-weaving spiders. *Definitions*: Spiders assume Fabian position in hot but not in cold weather. S denotes sunlight redirected onto the spider at about intensity of natural sunlight using a plane mirror (=*S*) or at greater or less than natural intensity using a concave mirror (>*S* or < *S*). The spider is simultaneously artificially shaded (*s*) or not (*S*). Numbers with * are considered alone, and numbers followed by common letters are considered together, to support strongly the thermoregulation hypothesis.

hypothesis (e.g. 1-7), while others support no other hypothesis (e.g. 15).

While the emphasis here has been on behaviours that reduce the heat load, spiders should use behaviours to warm them in order to enhance the time they are at optimal temperatures. This is the case in burrow dwelling lycosids (Humphreys, 1974, 1978, 1987a, 1987b) as well as in orb web spiders which may seasonally orientate their webs to maximise the projected surface area to warm more or faster (Carrell, 1978; Tolbert, 1979).

While there is an indication of size related effects in thermoregulatory behaviour in *Nephila* spp., as may be expected theoretically using a simple physical model, no such size effect was observed in *Stegodyphus lineatus* Latreille (Henschel *et al.*, 1992).

While the thermal behaviour of spiders is much more sophisticated than has been accepted, the presumed advantages of such fine tuning are not understood. None the less, the recognition of such behaviour is an important aspect of field studies and the means to do so are required, especially for smaller spiders which are intractable subjects for direct recording of temperature in the field. However, the sensible use of this schema should allow easy appraisal of the overt body positions of spiders in the field as to their likely thermoregulatory significance and it should assist in disentangling thermoregulatory from other behaviours.

A thermoregulator with the battery of finely graded behaviours seen here should, under ideal conditions, be able to maintain a near constant body temperature under a wide range of environmental conditions. In practice their temperatures fluctuate markedly with every air movement, at least partly owing to their small thermal capacity. If the spiders are innately incapable, owing to their small mass, of precise thermoregulation, why have they developed such a wide range of sophisticated behaviours which should permit precise thermoregulation?

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HYPERTROPHY OF MALE GENITALIA IN SOUTH AMERICAN AND AUSTRALIAN TRIAENONYCHIDAE (ARACHNIDA: OPILIONES: LANIATORES)

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Hunt, G.S. and Maury, E.A. 1993 11 11: Hypertrophy of male genitalia in South American and Australian Triaenonychidae (Arachnida: Opiliones: Laniatores). *Memoirs of the Queensland Museum* 33(2): 551-556. Brisbane. ISSN 0079-8835.

Hypertrophy of male genitalic elements, particularly the stylus, is described and discussed. A stylus is regarded as hypertrophied if stylus length is sub-equal to or longer than truncus length. Greatest hypertrophy occurs in the Australian species *Cluniella distincta* Forster (stylus x4.5 truncus) and a new genus, new species from South America (x2.5 truncus). Other species discussed are *Araucanobunus juberthiei* Muñoz-Cuevas from South America, and *C. minuta* Forster, *Rhynchobunus arrogans* Hickman, *Tasmanobunus parvus* Hickman, *Tasmanonuncia* sp., *Allobunus distinctus* Hickman and *Thelbunus mirabilis* Hickman from Australia. To accommodate an elongate stylus, the truncus is often shortened, and the genital operculum and sternum modified so that the genital orifice is located more anteriad. Hypertrophy of the stylus may be associated with the hypertrophy or reduction of other terminal elements. In *Cluniella* spp. and the two South American species penetration of the stylus occurs along a very long vagina; the spermathecae are situated at the base of the ovipositor. Hypertrophy may have evolved as a consequence of sexual selection. □*Opiliones, Triaenonychidae, male genitalia, hypertrophy, morphology, sexual selection.*

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The triaenonychid penis comprises a basal truncus supporting an apical complex which includes the stylus and associated plates, processes and setae. In the primitive condition, three sets of plates are present (Fig. 1A): the dorsolateral plates which are embryologically derived from the truncus and the dorsal plate and ventral plate embryologically related to the stylus (Martens, 1986). Both the dorsal and ventral plates were apparently primitively paired but are now fused, at least basally. The ventral plate carries setae. Certain taxa have undergone loss or reduction of plates (Martens, 1986; Hunt and Hickman, 1993). A few taxa have undergone extreme hypertrophy in the length of the stylus with one or more of the associated plates frequently showing correlated hypertrophy, or reduction, depending on the taxon.

HYPERTROPHIED STRUCTURES

CLUNIELLA SPP.

The most extreme hypertrophy of the stylus known for the family occurs in *Cluniella distincta* Forster, 1955 of SE Queensland and NE New South Wales (Fig. 2A). The stylus is x4.5 truncus length. There is correlated morphological change in the female where spermathecae occur basally in the ovipositor (Fig. 5C), unlike the usual condition where the spermathecae occur sub-apically. Therefore, the long stylus probably penetrates almost the whole length of the ovipositor to reach the spermathecae. The dorsolateral plates of the penis are elongate, gradually tapering to x2 ventral plate length (Fig. 2B). The dorsal plate is either lacking or intimately fused with the stylus; the latter is suggested by the subterminal lateral processes on the stylus which may be homologous to terminations of the dorsal plate (see *Thelbunus mirabilis* below, Fig. 5A). The ventral plate is reduced in size, and the number of inferior setae is reduced from three to two pairs.

The extreme stylus is accommodated within the body by shortening of the truncus, and by elongation of the genital operculum and posterior invagination of the sternum which together shift the genital opening anteriad. The sternum margins tend to follow the genital operculum (Fig. 5E; cf. female genitosternal region, Fig. 5F) but when the operculum is lifted the shape resembles that in Fig. 5H.

Cluniella minuta Forster, 1955, which overlaps in distribution with *C. distincta*, has undergone less radical elongation of the stylus (Figs 2C-D). Nevertheless, the stylus is x1.4 truncus length. The spermathecae are also basal despite the

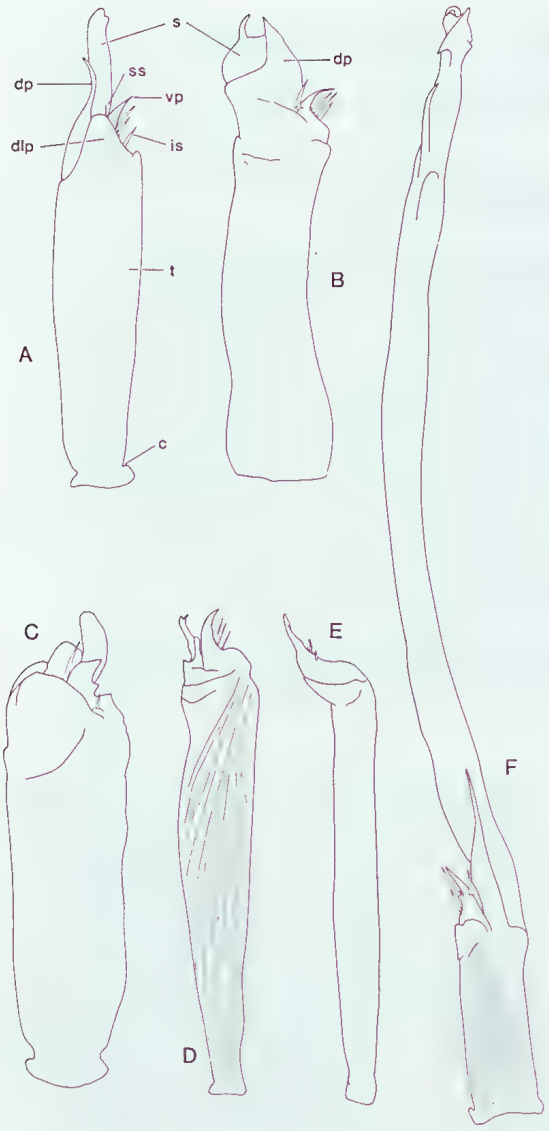


FIG. 1. Variation in ♂ genitalia of some Australian Triaenonychidae. A: *Hickmanoxyomma cavaticum*; B: *Glyptobunus signatus*; C: *Tasmanonyx montanus* D: *Dipristes serripus* (muscle shown); E: *Lomanella raniceps*; F: *Cluniella distincta* (muscle shown); c = constriction for membrane attachment; dlp =dorsolateral plate; dp = dorsal plate; is = inferior seta; s =stylus; ss =superior seta; t =truncus; vp =ventral plate.

shorter stylus. The dorsolateral plates are elongated to a similar extent to *C. distincta* while the ventral plate, though reduced, bears 3 pairs of inferior setae. The truncus is less shortened, the genital operculum is not elongate and the sternum is long and narrow. In both species, the constriction in the truncus where penis sheath membranes attach is basal.

The differences between the two species are not due to infraspecific variation, such as male dimorphism reported in some Australian genera (Hunt, 1985). Characters distinguishing *C. minuta* include a very long calcaneus compared with astragalus in leg I.

Araucanobunus juberthiei Muñoz-Cuevas, and New Genus, New Species (Maury, in prep.)

A. juberthiei from southern South America shows moderate hypertrophy of the stylus with stylus length about 1.3 truncus length (Figs 3A-B). An undescribed species referrable to a new genus (Maury, in prep.), but apparently with close genitalic affinities to *A. juberthiei*, has undergone greater hypertrophy with stylus length x2.5 truncus length (Fig. 3C). The dorsolateral plates are present in both species, but the dorsal plate is apparently lost (or intimately united with the stylus). The truncus in the undescribed species is greatly shortened, in *A. juberthiei* much less so.

Both species have an elongate genital operculum and a short, subtriangular sternum (for example, see Figs 5G-I). When closed, the genital operculum virtually obliterates the sternum.

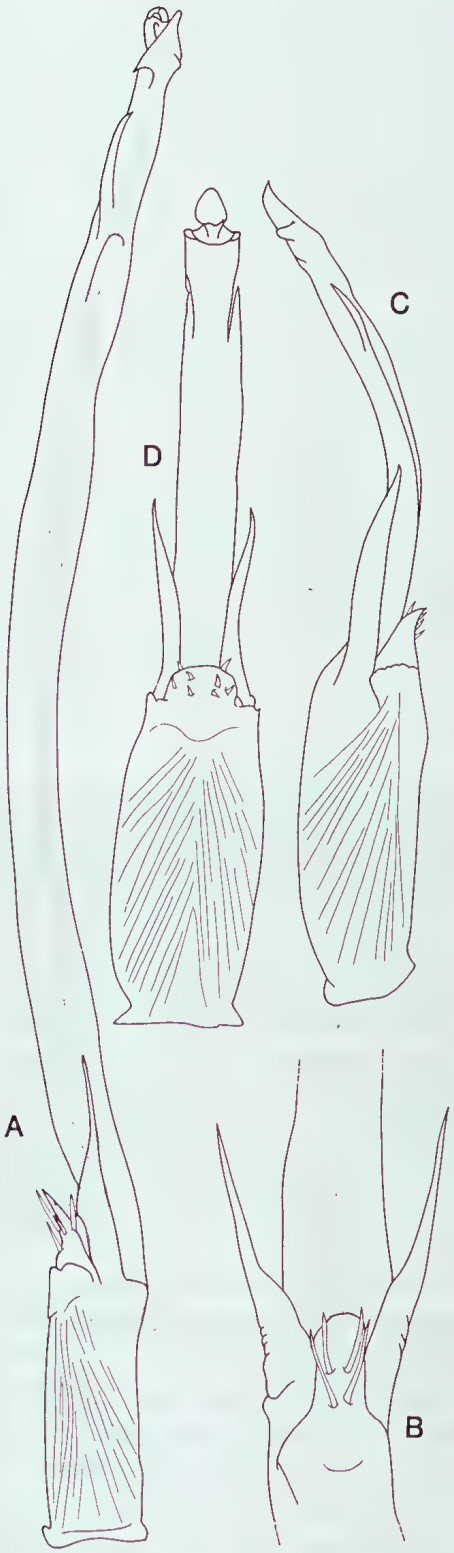
Unlike the condition in *Cluniella*, the constriction is situated mid-way along the truncus in both species (Figs 3A-D). As in *Cluniella*, the spermathecae are situated at the base of the ovipositor at the end of a long vagina (Fig. 5D: *A. juberthiei).* There appear to be no significant infraspecific variations in size or shape of the genitalia in these species.

Rhynchobunus arrogans Hickman

This species, from NE Tasmania, also has a prominent constriction at about mid-way along the truncus (Fig. 4A). *R. arrogans* belongs to a lineage distinguished by loss of the dorsolateral plates. The dorsal plate envelopes the stylus basally and terminates ventral to it. *R. arrogans* is very close to, if not congeneric with, *Glyptobunus signatus* Roewer (Hunt, in prep.). The stylus is x1.3 truncus length. The spermathecae are subterminal. The ventral plate is reduced but still carries the normal complement of setae for this lineage (Figs 4A-B). *R. arrogans* has an elongate genital operculum but lacks a triangular sternum.

Tasmanobunus parvus Hickman

This species is closely allied to, or possibly congeneric with, *R. arrogans* and *G. signatus* as



it lacks dorsolateral plates, its stylus carries a subdistal dorsal barb, and the dorsal plate terminates ventral to the stylus (Figs 4C-D). The stylus is subequal in length to the truncus and the dorsal plate has undergone complementary elongation. The constriction around the truncus is more subdued and situated somewhat more basally.

Tasmanonuncia n.sp.

This species belongs to the same general lineage as *R. arrogans* in that it lacks dorsolateral plates (Hunt, in prep.). However, the stylus carries a subdistal dorsal tuft of hairs instead of a single barb (Figs 4E-F). Stylus length is subequal to truncus length and, as with *Tasmanobunus parvus*, the dorsal plate is greatly elongate.

Allobunus distinctus Hickman

A. distinctus, from NW Tasmania, has a prominent constriction mid-way along the truncus. The stylus is modestly elongate, being subequal in length to the truncus. The ventral plate, however, is hypertrophied, uniting with other sclerotisations to form an elongate cylinder around the proximal half of the stylus (Figs 4G-H). The male of *A. distinctus* has a triangular sternum and a moderately elongate genital operculum.

Thelbunus mirabilis Hickman

Unlike the *Rhynchobunus* lineage, this NE Tasmanian species belongs to a lineage with well developed dorsolateral plates. The stylus is hypertrophied but the problem of space is partly solved by the stylus being twice folded back on itself (Fig. 5A). The dorsal plate is also elongate and closely integrated with the stylus, bifurcating into two lobes just below the stylus tip. The ventral plate setae are greatly hypertrophied and differentiated into different forms (Fig. 5B). This species also has a short triangular sternum (though not unlike the female) and an elongate genital operculum (Figs 5J-K).

Thelbunus n.sp. has a less elaborate stylus and its sternum less modified and genital operculum less elongate (sternum illustrated in Fig. 6).

Other Opiliones

Hypertrophy of the stylus has also been recorded in the neopilionid *Ballarra* spp (suborder Palpatores) from Australia (Hunt and Coken-

FIG. 2. Hypertrophied ♂ genitalia of *Cluniella* spp. A, B: *C. distincta*, A = lateral, B = ventral view of ventral and dorsolateral plates. C, D: *C. minuta*, lateral and ventral.

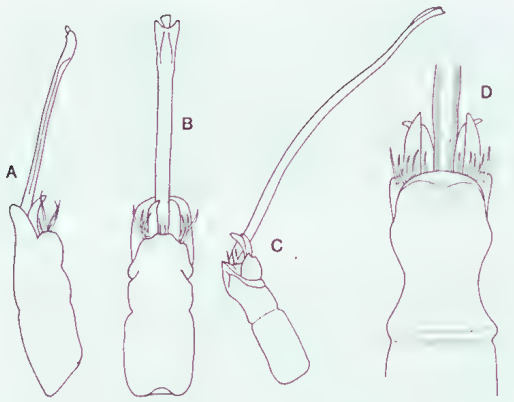


FIG. 3. Hypertrophied ♂ genitalia of South American Triaenonychidae. A, B: *Araucanobunus juberthiei*, lateral and ventral. C, D: New genus, new species (Maury, in prep.), lateral, ventral (part).

dolpher, 1991). Unlike the situation in *Cluniella* spp. and the South American species, the spermathecae are greatly elongate, opening into a short vagina but ending basally in the ovipositor. The long stylus is presumably inserted down the elongate spermatheca, not an elongate vagina as occurs in *Cluniella*.

Other taxa exhibit elongation of the truncus, e.g., many species of the triaenonychid genus *Lomanella* (Hunt and Hickman, 1993).

DISCUSSION

An elongate stylus is frequently, but not invariably, associated with an elongation of the genital operculum and a shortening and broadening of the sternum which together serve to elongate the cavity in which the penis lies (also, shortening of the truncus may compensate for the elongate stylus).

These changes in genitosternal architecture seem to have arisen independently in several distantly related gerera. Within the one genus, both normal and hypertrophy-related genitosternal architecture can occur. For example, *Cluniella minuta* has evolved a moderately elongate stylus while retaining a 'normal' long, narrow sternum and rounded genital operculum. *C. distincta* has undergone much greater elongation of the stylus with consequent changes in the sternum and genital operculum.

It seems more probable that the situation in *C. minuta* is more 'primitive', while the syndrome of extreme characters in *C. distincta* represents a more derived condition. Thus, in the *Cluniella* lineage, space limitations of an elongate stylus

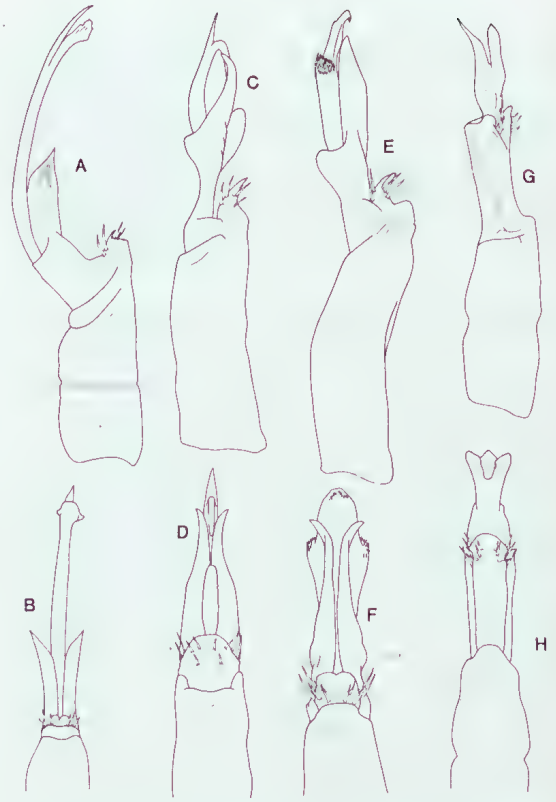


FIG. 4. Hypertrophied ♂ genitalia in Tasmanian Triaenonychidae. A, B: *Rhynchobunus arrogans*, lateral and ventral. C, D: *Tasmanobunus parvus*, lateral and ventral. E, F: *Tasmanonuncia* n.sp. (Hunt, in prep.), lateral and ventral. G, H: *Allobunus distinctus*, lateral and ventral.

seem initially accommodated by shortening of the truncus (*C. minuta* condition). Changes to the genital operculum and sternum evolved later.

Cluniella spp. and the two South American species described above show close correspondence in many features associated with stylus hypertrophy: great elongation of stylus, modification of sternum and genital operculum, shortening of truncus, and spermathecae situated basally in the ovipositor at the end of a very long vagina.

The question is whether these features indicate a close phylogenetic relationship or whether they are examples of convergence. The latter is supported because:

1. Modifications to genitosternal architecture appear to have arisen independently within the *Cluniella* lineage, evolving from the 'normal' condition as occurs in *C. minuta*.

2. Attachment of penis sheaths is basal in *Cluniella* and mesial in South American species.

3. The penes of the South American species

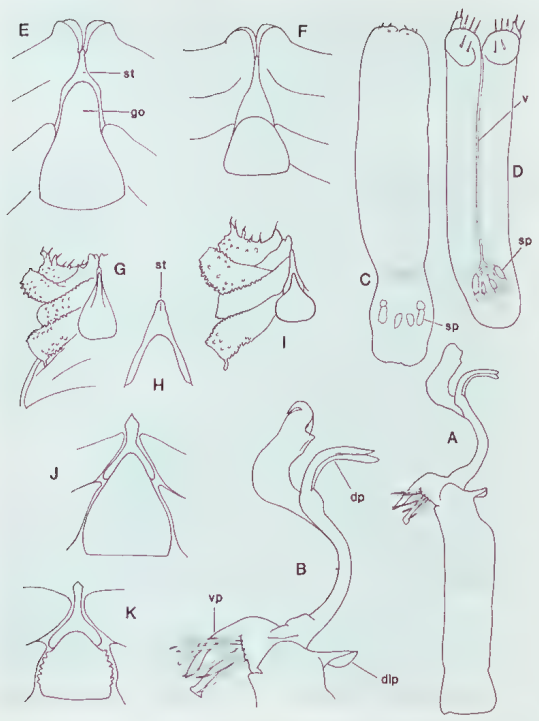


FIG. 5. Hypertrophy of genitalia in *Thelbunus mirabilis* and modified structures associated with genitalic hypertrophy in various Triaenonychidae. A, B: *T. mirabilis*, lateral and detail of lateral showing hypertrophy and modification of ventral plate setae. C,D: Ovipositor in *Cluniella distincta* and *Araucanobunus juberthiei* respectively showing basal seminal receptacles. E, F: Genitosternal region of *C. distincta*, ♂ and ♀ respectively. G, I: Genitosternal region of South American new genus, new species (Maury, in prep.), ♂ and ♀ respectively; H = shape of sternum in ♂ after genital operculum removed. J, K: genitosternal region of *T. mirabilis*, ♂ and ♀ respectively; go = genital operculum; sp = spermatheca; st = sternum; v = vagina (not delineated in *C. distincta*).

show closer affinity with the South American genus *Triaenonychoides* (see Maury, 1987)) rather than with Australian genera.

4. Apart from the basal spermathecae and long vagina, the ovipositor of the South American species appears to be of the typical triaenonychid form. The ovipositor of both *Cluniella* spp. is highly derived in having a very membranous tip, in lacking well developed sensory lobes, and in carrying vestigial setae. In some specimens examined the membranous tip was inflated and had 'ballooned' out the genital orifice. This morphology suggests that the female may assist penetration by inflating the ovipositor so that it partly engulfs the stylus. Thus, assuming that the male *C. minuta* has not undergone a reversal in genitosternal architecture, the derived ovipositor seems to have evolved before shortening of the male sternum and elongation of the genital operculum.

Thus, the genomes of *Cluniella* and the two South American taxa have the capacity to allow quite remarkable convergence in a syndrome of characters. The overall effect appears the same, but the details differ.

Why have such vastly elongate styluses evolved, particularly to the extreme shown by *C. distincta*? Sexual selection by female choice is favoured by Eberhard (1985) as the most generally applicable explanation for 'extravagant' genitalia. Eberhard proposes that 'male genitalia function as 'internal courtship'. devices to increase the likelihood that females will actually use a given male's sperm to fertilize her eggs rather than those of another male'. In the case of *Cluniella* and the South American species, it is postulated that males with the largest styluses have greater success than males with smaller styluses and hence contribute more of their genes to the next generation. The genitalia may stimulate the female prior to or during copulation and so activate the appropriate responses, or it might provide the right mechanical and sensory 'fit' during copulation. The basal spermathecae in the ovipositor of *Cluniella* spp. and the two South American species (and the long stylus matching the long spermathecae in *Ballarra* spp.) suggest that the correct mechanical fit may at least be part of the answer.

A search for congeners and an analysis of inter- and intraspecific variation, as well as behavioural studies, may yield further data to resolve these questions.

ACKNOWLEDGEMENTS

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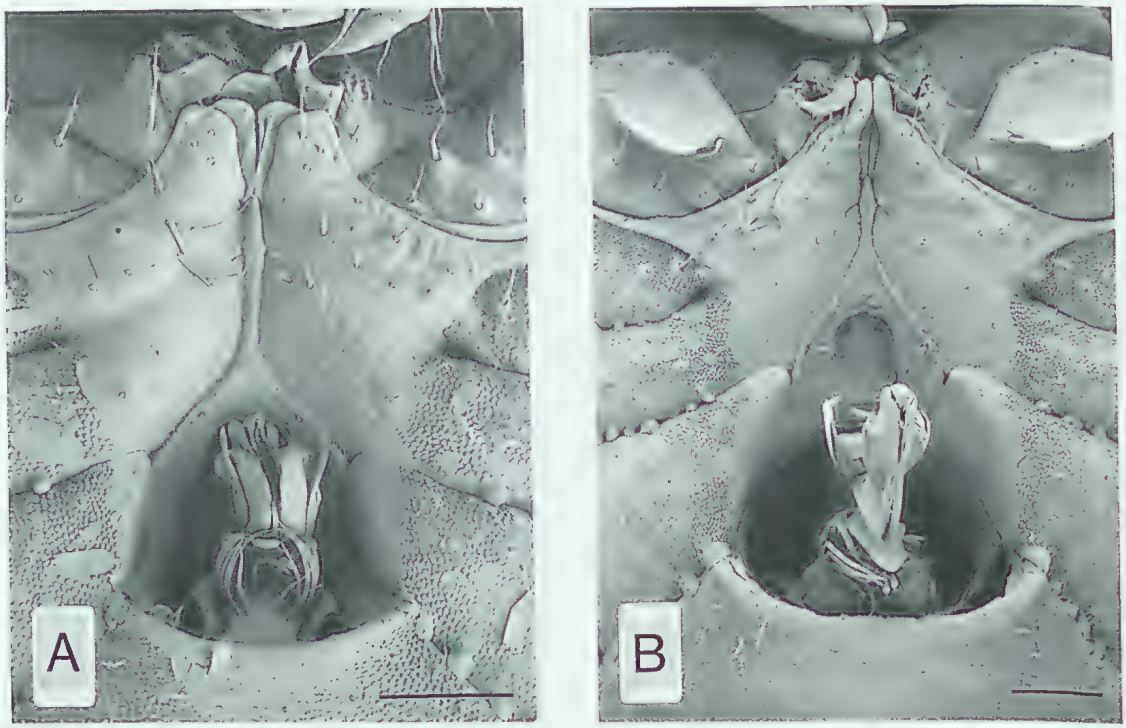

FIG. 6. Genitosternal region in *Thelbunus* spp. and variation in sternum; A = sp. nov.; B = *T. mirabilis*. Genital operculum lifted; note recess in sternum where folded stylus fits. Scale bars= 500μm.

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PREDATOR-PREY CO-EVOLUTION OF *PORTIA FIMBRIATA* AND *EURYATTUS* SP., JUMPING SPIDERS FROM QUEENSLAND

ROBERT R. JACKSON AND R. STIMSON WILCOX

Jackson, R.R. and Wilcox, R.S. 1993 11 11: Predator-prey co-evolution of *Portia fimbriata* and *Euryattus* sp., jumping spiders from Queensland. *Memoirs of the Queensland Museum* **33**(2): 557-560. Brisbane. ISSN 0079-8835.

Portia is a salticid that preys on other spiders and *Euryattus* sp. is a salticid that nests inside suspended rolled-up leaves. *Portia* and *Euryattus* are sympatric at a site near Cairns but not known to be sympatric at other sites studied. *Portia* from the Cairns site practices a unique prey-specific predatory behaviour against *Euryattus*, and *Euryattus* from this site is efficient at detecting and defending itself against *Portia*. *Euryattus*, but not *Portia*, is present at a site near Davies Creek which, although only ca 15km from the Cairns site, is more xeric and at a higher elevation. Three types of tests were carried out to compare *Portia*'s efficiency at catching adult allopatric versus sympatric *Euryattus* (Test 1), allopatric *Euryattus* juveniles versus juveniles of another salticid species on which *Portia* is known to prey (Test 2) and allopatric versus sympatric *Euryattus* juveniles (Test 3). In these tests, *Portia* behaved similarly toward allopatric (Davies Creek) and sympatric (Cairns) *Euryattus*, except that it attacked and killed allopatric more often than sympatric *Euryattus*. Allopatric *Euryattus*, in contrast to Cairns *Euryattus*, appeared not to recognize an approaching *Portia* as a predator.□*Portia fimbriata, Euryattus, Jacksonoides, co-evolution, allopatry, sympatry.*

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Portia is a genus of specialized jumping spiders (Salticidae) that prey on other spiders (Jackson and Hallas, 1986). *Portia* is a detritus mimic and has a unique, slow, choppy style of locomotion that seems to preserve its crypsis. There are seven described species of *Portia*, distributed in the tropics of Africa, Asia, and Australasia (Wanless, 1978). A population of *Portia fimbriata* (Doleschall) in Queensland uses specialized behaviour to catch other species of salticids (Jackson and Blest, 1982). This population of *P. fimbriata* also uses a prey-specific predatory behaviour against females of a particular sympatric salticid, *Euryattus* sp. (Jackson and Wilcox, 1990).

Euryattus females suspend a dead, rolled-up leaf by strong guylines from rock ledges and tree trunks, then use the leaf as a nest (Jackson, 1985). *Portia* has never been observed to attempt to catch *Euryattus* by going inside the rolled-up leaf. However, in Queensland, *P. fimbriata* uses vibratory displays to lure *Euryattus* females from their nests (Jackson and Wilcox, 1990). These displays apparently mimic courtship displays of *Euryattus* males (Wilcox and Jackson, unpubl. data). Other species of *Portia* and populations of *P. fimbriata* in areas from which *Euryattus* is absent do not perform these displays (Jackson and Wilcox, 1990).

Queensland *P. fimbriata* will wait for hours at a time for *Euryattus* to come out of its nest (Jackson and Wilcox, 1990). Often, *Euryattus* actively defends itself by leaping at *Portia* and driving it away (Jackson and Wilcox, 1990). This is unusual behaviour for a salticid. From thousands of observations of interactions between *P. fimbriata* and many different species of salticids (Jackson and Hallas, 1986), it is evident that *Euryattus* is more efficient than other salticids at recognizing and defending itself against an approaching *Portia*. Also, in laboratory tests (Jackson and Wilcox, 1990), *Euryattus* readily recognized an approaching *Portia* as a potential predator, whereas *Jacksonoides queenslandica*, another salticid on which *P. fimbriata* feeds (Jackson and Blest, 1982), did not recognize *P. fimbriata*. This suggests an evolutionary 'arms race' (sensu Dawkins and Krebs, 1979) between *Euryattus* and *P. fimbriata*. Frequent predation by *P. fimbriata* on *Euryattus* may have favoured special abilities in *Euryattus* to recognize and defend itself against *P. fimbriata*. This, in turn, may have resulted in the evolution of refinements of *P. fimbriata*'s predatory behaviour. To test this hypothesis, we must compare the behaviour of *Euryattus* in populations with and without *Portia*. Recently, such an opportunity arose when *Euryattus* were found in an area in which *Portia* was not known.

MATERIALS AND METHODS

Cages, maintenance, terminology, basic testing procedures and analysis are given in Jackson and Wilcox (1990). Laboratory cultures of sympatric *Euryattus*, *J. queenslandica* and *P. fimbriata* were established, using spiders collected from rainforest near Cairns at about sea level (see Jackson, 1985; Jackson and Hallas, 1986). A laboratory culture of allopatric *Euryattus* was established from spiders collected in an *Acacia-Eucalyptus* woodland beside Davies Creek, near Davies Creek National Park in the Atherton Tableland (about 15km from the study site near Cairns and at c. 500m elevation). *Portia* has never been recorded from this and other Atherton Tableland habitats (Wanless, 1978; Jackson, unpubl. data). Unless noted otherwise, all spiders tested were reared in the laboratory from eggs of field-collected spiders. No individual spiders were used in more than one test. In this paper, we refer to *Euryattus* from Cairns and Davies Creek as 'sympatric *Euryattus*' and 'allopatric *Euryattus*', respectively. There were no evident differences related to general behaviour between these two populations of *Euryattus*. In particular, similar leaves were suspended by females for nests and males courted with similar vibratory displays.

The systematics of the genus *Euryattus* remains uncertain. Whether the two populations of *Euryattus* we studied are one or two different species is not now known. Voucher specimens were deposited at the Florida Collection of Arthropods (Gainesville) and the Queensland Museum.

We conducted three tests. In Test 1, *Portia* was given access to an adult allopatric *Euryattus* female in her nest. In Test 2, on alternate days, *Portia* was given access to a juvenile (2-3mm in body length) allopatric *Euryattus* and a juvenile (2-3mm) *J. queenslandica* in a bare cage (i.e., no nest or other objects present). In Test 3, on alternate days, *Portia* had access to a juvenile (2-3mm) of an allopatric and a juvenile of a sympatric *Euryattus* in a bare cage. To begin each type of test, *Portia* was placed into a cage containing the other spider shortly after lights came on in the laboratory (0800 hours). Spiders were observed continuously until predation occurred or until 4h had elapsed. Each test was either identical or at least similar to tests carried out previously (Jackson and Wilcox, 1990).

Data from Test 1 using allopatric *Euryattus* adults were compared to data from the identical type of tests using sympatric *Euryattus* adults in an earlier study (Jackson and Wilcox, 1990) to see whether *Portia*'s capture efficiency against allopatric *Euryattus* adults was greater than against sympatric *Euryattus* adults. Test 2 using allopatric *Euryattus* juveniles was compared to type 2 tests in Jackson and Wilcox (1990) using sympatric *Euryattus* juveniles and *J. queenslandica* juveniles. We already know that *Portia* captures *J. queenslandica* juveniles more efficiently than it captures sympatric *Euryattus* juveniles (Jackson and Wilcox, 1990). Here we examine whether *Portia*'s capture efficiencies against these two salticids vary when *Euryattus* is allopatric. Test 3 enabled us to compare *Portia*'s efficiency at capturing allopatric and sympatric *Euryattus* juveniles.

Adult body length is c.8mm for both *J. queenslandica* and *P. fimbriata* and for both populations of *Euryattus*. Jackson and Wilcox (1990) used three size classes, defined by the ratio of prey to predator body volume, when testing *P. fimbriata* with juvenile salticids: small (0.1-0.25), medium (0.5-1), and large (1.5-2). Only two of these (medium and large) were used here.

McNemar tests for significance of changes were used for statistical analyses of the results from Tests 2 and 3, these tests being designed as paired comparisons (Sokal and Rohlf, 1981): each individual *Portia* was used in one test with one salticid and another test with the other salticid 48 h earlier or later (decided randomly). Yates' corrections were applied to the McNemar tests, and the Bonferroni adjustment (see Rice, 1989) was made to significance levels whenever single data sets were used in multiple comparisons.

RESULTS

Test 1: *Euryattus* Adult in Nest

P. fimbriata behaved similarly toward allopatric (herein) and sympatric (Jackson and Wilcox, 1990) *Euryattus*, except that it attacked and killed allopatric *Euryattus* more frequently than sympatric *Euryattus* (Fig. 1, test of independence, $P<0.01$). Allopatric *Euryattus* appeared less prone than sympatric *Euryattus* to recognize *P. fimbriata* as a predator: 85% of the *P. fimbriata* got onto the leaf with allopatric *Euryattus*, but only 43% got onto the leaf with sympatric *Euryattus*; 23% of sympatric *Euryattus*, but only 4% of allopatric *Euryattus*, drove *P. fimbriata* away (Fig. 1).

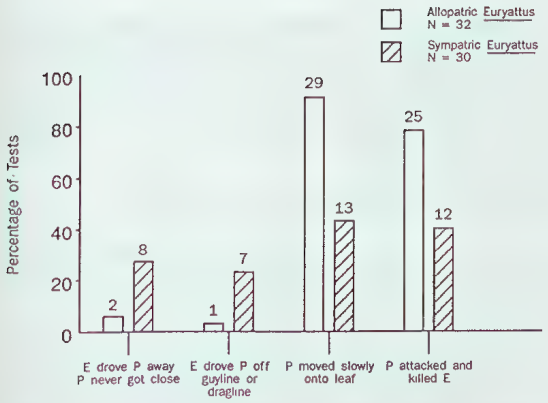

FIG. 1. *P. fimbriata* (P) tested with adult allopatric (Davies Creek) and sympatric (Crystal Cascades) *Euryattus* females (E) in suspended, rolled-up leaves. Data for sympatric *Euryattus* from Jackson and Wilcox (1990). Close: on leaf or guyline connected to leaf, or dropping on dragline toward leaf. For each outcome of test, number given above bar and percentage is read from axis.

Test 2: Juvenile *Euryattus* and *Jacksonoides queenslandica*

There was no evidence that *Portia* captured or stalked *J. queenslandica* more frequently than allopatric *Euryattus* (Figs 2, 3, McNemar tests, NS). Allopatric *Euryattus* did not appear to recognize *Portia* as a predator any more readily than did *J. queenslandica*.

Test 3: Cairns and Davies Creek *Euryattus* Juveniles

There was no evidence that *Portia* stalked sympatric *Euryattus* any more frequently than allopatric *Euryattus*, but *Portia* caught allopatric

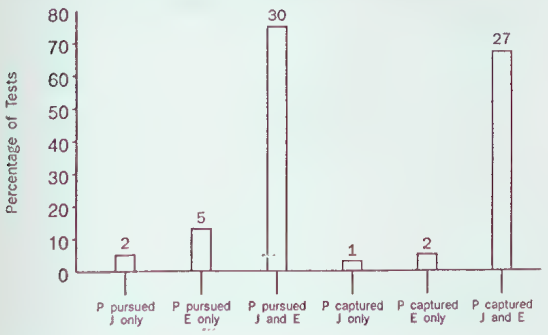

FIG. 2. Responses of *P. fimbriata* (P) to medium size (see text) allopatric *Euryattus* (E) and sympatric *J. queenslandica* (J). 40 paired tests: each *Portia* tested with one *Euryattus* and, on an alternate day, with one *Jacksonoides* (see text). Data for 'P pursued neither J nor E' and 'P captured neither J nor E' not displayed.

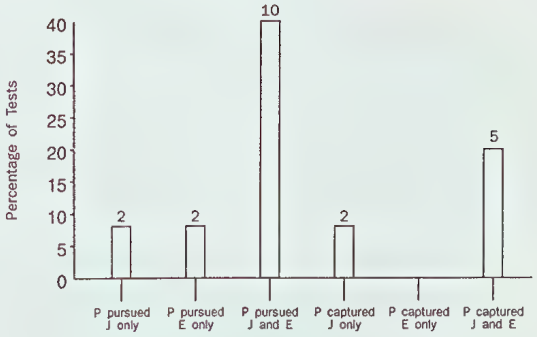

FIG. 3. Responses of *P. fimbriata* (P) tested with large (see text) allopatric *Euryattus* (E) and sympatric *J. queenslandica* (J). 25 paired tests: each *Portia* tested with one *Euryattus* and, on an alternate day, with one *Jacksonoides* (see text). Data for 'P pursued neither J nor E' and 'P captured neither J nor E' not displayed.

Euryattus more often that it caught sympatric *Euryattus* (Figs 4, 5).

DISCUSSION

Only one population of *Portia fimbriata* from Cairns studied (Jackson and Wilcox, 1990) is sympatric with *Euryattus*. *Euryattus* suspends a rolled-up leaf for a nest, and this is the only salticid sympatric with the Cairns *Portia*, or with any other *Portia* studied, known to do this. Only the Cairns *Portia* is known to use a prey-specific predatory behaviour against *Euryattus*. The sympatric (Jackson and Wilcox, 1990), but not the allopatric, *Euryattus* appears readily to recognize and defend itself against *Portia*. In fact, the al-

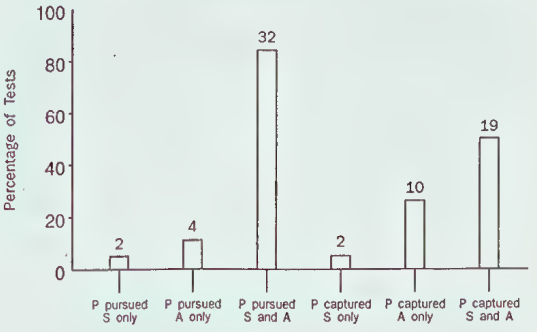

FIG. 4. Responses of *P. fimbriata* (P) to medium size (see text) sympatric (S) and allopatric (A) *Euryattus* sp. juveniles. 38 paired tests: each *Portia* tested with one sympatric and, on an alternate day, with one allopatric *Euryattus* (see text). Data for 'P pursued neither S nor A' and 'P captured neither S nor A' not displayed.

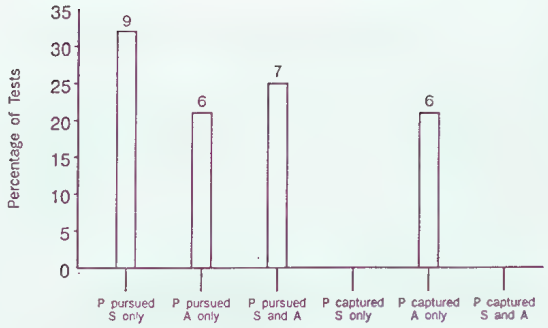

FIG. 5. Responses of *P. fimbriata* (P) to large (see text) sympatric (S) and allopatric (A) *Euryattus* sp. juveniles. 28 paired tests: each *Portia* tested with one sympatric and, on an alternate day, with one allopatric *Euryattus* (see text). Data for 'P pursued neither S nor A' and 'P captured neither S nor A' not displayed.

lopatric *Euryattus* appears to be no better than *J. queenslandica* at escaping predation by *Portia* , whereas *Portia* captured *J. queenslandica* more efficiently than it captured the sympatric *Euryattus* (Jackson and Wilcox, 1990). The ability of the Cairns *Euryattus* appears to be a predator-specific antipredator behaviour.

Population differences were evident despite there being no known prior experience of the predator by the prey or the prey by the predator under laboratory rearing conditions in this and the earlier (Jackson and Wilcox, 1990) study. These findings suggest that, in the Cairns area, *Portia* and *Euryattus* appear to have acted as selective agents on the evolution of each other's behaviour.

ACKNOWLEDGEMENTS

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"WE'LL MEET AGAIN", AN EXPRESSION REMARKABLY APPLICABLE TO THE HISTORICAL BIOGEOGRAPHY OF AUSTRALIAN ZODARIIDAE (ARANEAE)

R. JOCQUÉ

Jocqué, R. 1993 11 11: "We'll meet again", an expression remarkably applicable to the historical biogeography of Australian Zodariidae (Araneae). *Memoirs of the Queensland Museum* 33: 561-564. Brisbane. ISSN 0079-8835.

The largest subfamily of the Zodariidae, the Zodariinae, contains 31 genera and has endemic representatives on all tropical continents. The sequence in this clade first indicates that the Australian zodariid fauna is the result of a combination of vicariance and dispersal events. Only three zodariid genera are not endemic to Australia. It is argued that two of these, *Mallinella* and *Asceua*, have reached Australia by dispersal over forest-covered areas. It is remarkable that the endemic Australian genera in the Zodariinae are more closely related to the African ones than are the Neotropical genera which is in contrast with the current ideas on chronology in plate tectonics. A possible explanation might be found in the past and present distribution of forests. The appearance of this type of vegetation on the Cretaceous-Tertiary boundary, might also be invoked to explain bipolar distributions in Africa.

La plus importante des sous-familles des Zodariidae, les Zodariinae, contient 31 genres, dont des endémiques sur chaque continent tropical. La séquence dans ce grand clade indique d'abord que la composition de la faune australienne serait le résultat d'une combinaison de vicariance et de dispersion. Seuls trois genres trouvés en Australie n'y sont pas endémiques. On avance l'argument selon lequel deux d'entre eux ont réussi à atteindre l'Australie par dispersion à travers des aires couvertes de forêts. Il est remarquable que les genres endémiques australiens soient plus proches des genres africains que de ceux d' Amérique du Sud ce qui contredit les idées courantes concernant la chronologie de la dérive des plaques. Une explication possible pourrait se trouver dans la distribution passée et actuelle des forêts équatoriales. La génèse de ce type de végétation, à la fin du Crétacé, pourrait également expliquer la distribution bipolaire de certaines vieilles lignées d'invertébrés. □*Africa, Gondwanaland, distribution, vicariance.*

Rudy Jocqué, Koninklijk Museum voor Midden-Afrika, B-3080 Tervuren, Belgium; 13 October, 1992.

The Zodariidae are a medium-size pantropical family of mainly nocturnal, ground-living spiders. Except for the members of the subfamily Storenomorphinae they are virtually all burrowers to some degree. Some simply dive into sand (*Psammoduon*) or hide in litter (*Asceua, Mallinella*) whereas others make a complex retreat consisting of a burrow with a trapdoor (*Psammorygma, Neostorena*) or an igloo-like construction of pebbles or grains of sand (*Diores, Zodarion*). This sedentary lifestyle and the fact that zodariids do not balloon explains why most species have small distribution ranges. It also makes them an ideal subject for zoogeographical studies, moreover since a cladistic analysis of the family is available (Jocqué, 1991).

THE AUSTRALIAN ZODARIIDAE

Most Australian zodariids, estimated at several hundred species, belong to genera endemic to the Australian continent. There is no trace of any representatives of these genera on any other continent (Table 1).

Genus	Distribution	Habitat
Asceua	Palaeotropics & Australia	circumforest
Asteron	Australia	steppe -woodland
Cyrioctea	southern Gondwana	dunes
Habronestes	Australia	steppe -woodland
Ishania	South and Central America	circumforest
Mallinella	Palaeotropics & Australia	tropical forest
Neostorena	Australia	steppe -woodland
Storena	Australia	steppe -woodland
Storosa	Australia	steppe -woodland
Tenedos	South and Central America	steppe -circumforest

TABLE 1. Distribution and habitat of some zodariid genera.

Three genera have representatives elsewhere and in fact have the centre of their distribution outside Australia. The first one is *Cyrioctea*, the only genus in the Cyriocteninae, found exclusively in sandy habitats such as arid dunes and sand deserts. It has a typical Gondwanan distribution

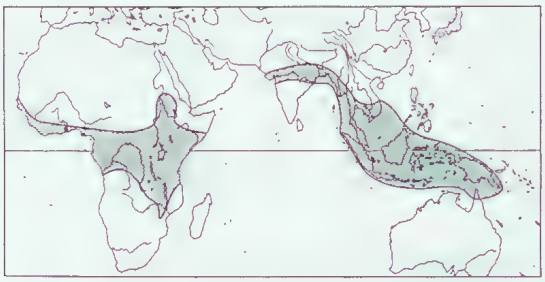

FIG. 1. Approximate distribution of *Mallinella*.

with representatives in South Africa, Chile and Australia (*Cyrioctea raveni* Platnick and Griffin). Both the other genera, *Mallinella* and *Asceua*, have an enormous distribution which appears to be linked with old world forests. One species of each has reached the northern tip of Australia.

The Australian zodariid fauna is thus apparently composed of three different stocks: a strictly endemic one, a southern Gondwanan one and a third element that could be quoted as old world forest fauna. To understand this composition we have to go back to an era before the breakup of Gondwanaland.

The Zodariidae indeed have a basic Gondwanan distribution with the more plesiomorphic taxa represented in Africa, Australia and South America. These are the Cyriocteinae, the Lachesaninae and the more plesiomorphic members of the Zodariinae. The latter taxon is now known to include what has been described as the subfamily Storeninae (Jocqué, 1991, 1992). Thirty-one out of 47 genera now belong in the Zodariinae. However, the more apomorphic members of the subfamily (Femoral Gland Clade or FGC), having several synapomorphies (femoral gland, lack of chilum, flattened incised hairs, fused chelicerae) are present only in Africa (including part of the Palaearctic) and tropical Asia. The same applies to the Storenomorphinae and the Cydrelinae which are restricted to tropical Africa and tropical Asia.

When Africa got finally separated from other major landmasses, slightly more than 100 mybp, these three groups were apparently not yet in existence. The bulk of the zodariid fauna outside that continent is therefore supposed to be derived of the plesiomorphic taxa present at the time of the split-off. However, from the above it is clear that India (and part of South East Asia ?) carried a much more modern assemblage of Zodariidae when it moved towards its present position. Indeed, there is no evidence that at least purely tropical forest organisms (e.g., *Mallinella*) originating in Africa, have been able to reach India via a northern itinerary. No forest connection has ever existed via the mediterranean and the Arabian peninsula. This paradox is discussed below.

Virtually all Zodariidae are restricted to habitats lying in a climatic zone with a marked dry season. In the Neotropics only a few species (in *Ishania* and *Tenedos*) seem to have adapted to moist forest and no zodariids have so far been found in Amazonia. In Australia no true forest-inhabiting species belonging to endemic genera appear to be present, although some species in the genera *Neostorena*, *Asteron*, *Storosa* and *Habronestes*, occur in dense woodland. But the most common and widely distributed forest inhabiting genus is doubtlessly *Mallinella*. This genus has an enormous distribution (Fig. 1): it occurs in virtually all African forests from Senegal in the west to the Chimanimani Mts. (Zimbabwe) (Jocqué, unpublished data) in the south and Kenya and Ethiopia in the east, but is remarkably absent from the South African forests which emphasizes its inability to cross unforested zones. It is present in montane rainforest in India and Nepal and occurs in virtually all dense forests in the Far East, as far as New Guinea. One species has reached the northeastern tip of Australia. This is apparently a very recent event as that species, *Mallinella zebra* Thorell, occurs on both New Guinea and Australia. Considering the fractionating of this genus in the rest of its distribution range and the fact that no speciation has occurred in this case, there is little doubt that the arrival occurred during the Pleistocene ice-ages, during which there was a land-bridge linking New-Guinea and Australia (Keast, 1983). A well documented case of a less recent Asian invader is that of *Tamopsis* (Hersiliidae) which is supposed to have arrived in northern Australia during the Miocene (Baehr, 1988). This relatively early arrival has resulted in clockwise colonization of almost the entire circumference of the Australian continent and the appearance of many strongly related species.

A second recent zodariid arrival is that of an undescribed species of *Asceua* (Jocqué, in preparation) which can be characterized as a circum-forest genus. Its ecological status is fairly similar to those genera mentioned above, which occasionally occur in dense woodland or even rainforest in the case of the South American *Ishania* and *Tenedos*. The distribution of *Asceua* (Fig. 2) is even larger than that of *Mallinella* and

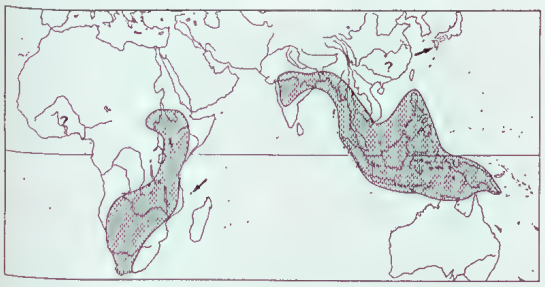

FIG. 2. Approximate distribution of *Asceua.*

the patterns overlap only partially. Although several Asian species are known to occur in rainforest (Bosmans and Hillyard, 1990; P. Schweninger pers. comm. 1989; C. Deeleman-Reinhold, pers. comm. 1988; J. Murphy, pers. com. 1988) no representatives are found in African lowland rainforest. On the other hand it is present in rather dry areas in southern Africa. Considering its very restricted distribution area in Australia, it is supposed to have arrived there at the same time as *Mallinella.*

Two closely related lines of zodariines which had been separated for about a hundred million years thus met again.

Assuming that *Mallinella* was initially better adapted to rainforest conditions, it would be interesting to study if the arrival of *Mallinella zebra* has induced a shift in the rest of the zodariid fauna in the area it now occupies, and whether it is still expanding.

GENERAL DISTRIBUTION OF THE ZODARIINAE

The monophyletic assemblage of the Zodariinae is largely composed of genera which are endemic to particular continents (Jocqué 1991, fig. 41). Remarkably, the African genera are apparently more closely related to the Australian Zodariinae than to those in South America. The five Neotropical genera are indeed near the root of the zodariine branch whereas the Australian ones are situated in between the Afrotropical and the Palaeotropical ones (the latter group has an apparently recent outflow into the Palaearctic). The reduced area-cladogram resulting from these relationships is given in Fig. 3. This statement is at least puzzling: it is in contrast with the timing of major plate tectonic events that caused the breakup of Gondwanaland, as deduced from geological data and corroborated by many biogeographical data (e.g. Nelson and Platnick, 1980). However, not only is there much controversy about the original position of many plates, the timing and the mechanics of the movement are also subject to a debate. The expansion theory of Carey (1975) and Shields (1979, 1983) positions several plates in different places than does the classical theory (Norton and Sclater, 1979; Owen, 1983). According to the latest data (Veevers *et al.*, 1991; Scotese *et al.*, 1988; Powell *et al.*, 1988) it appears that India split off from Gondwanaland together with the southern continents Australia and Antarctica. How then can one explain the fact that India and Sri Lanka share many apomorphic monophyletic taxa with Africa (e.g., *Hermippus*, Storenomorphinae, Cydrelinae, members of the FGC)? Briggs (1987) thinks that India, on its course to Asia, became again attached to north-east Africa by the end of the Cretaceous, a remarkable hypothesis that might explain the apparent faunal anomaly. It would certainly explain how forest dwelling spiders like *Mallinella* and *Asceua* have reached Asia.

The main question that is raised by the zodariid cladogram is why the Australian taxa are more strongly related to the African than to the South American ones.

A possible explanation is that the few typical forest inhabiting zodariid genera did only evolve after the main continents had broken away from Africa. Broad-leaved forests arose at least during the Cretaceous but became dominant in equatorial conditions on the Cretaceous-Tertiary boundary (Wolfe, 1987; Wolfe and Upchurch, 1986, 1987). It is strange that in the context of African biogeography no mention has been made of the dramatic shift that has been brought about by the appearance of broad-leaved evergreen forest. The conditions at ground level in this kind of forest and the former conifer forests were probably as different as they are for instance in present-day rainforest and miombo in Africa. The faunas of these vegetation types are equally very different. Dense miombo woodland and submontane evergreen forest within each other's sight on the Nyika Plateau in Malawi, contain completely different litter-layer spider faunas with hardly any genus overlap in the spider families that have been studied (Zodariidae, Linyphiidae, Lycosidae, Tetragnathidae; Jocqué, unpublished data).

The present day bipolar distribution of many ancient African taxa of ground-dwelling invertebrates might therefore be explained in the light of the evolution of broad-leaved rain forest

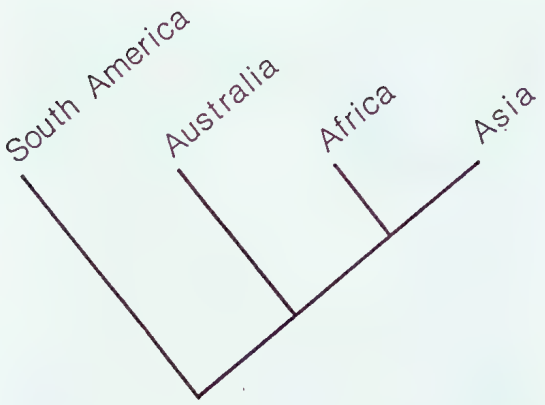

FIG. 3. Area cladogram of tropical continents as based on the clade of the Zodariinae.

during the Cretaceous. This novel type of vegetation with a very new structure and hence ecological conditions, split most existing taxocoenoses that had to adapt to the new forest conditions. In the Zodariidae only very few genera succeeded in doing so. In Africa only *Mallinella* really developed into a specialised forest spider genus.

The remote relationship of South American and African Zodariidae may well be the result of similar events at the time of the breakup of Gondwanaland favouring the dispersion of particular genera, hampering that of others.

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BASIC ARCHITECTURE OF THE OVARY IN THE GOLDEN SILK SPIDER, *NEPHILA CLAVATA*

AKIO KONDO, EIKO CHAKI AND MITSUHIRO FUKUDA

Kondo, A., Chaki, E. and Fukuda, M. 1993 11 11: Basic architecture of the ovary in the golden silk spider, *Nephila clavata*. *Memoirs of the Queensland Museum* 33 (2): 565-570. Brisbane. ISSN 0079-8835.

In gravid females of the golden silk spider, *Nephila clavata* L. Koch, the ovaries are composed of flat cisternae. To clarify whether the cisternal structure is primarily or secondarily formed by pressure from mature eggs, ovary development was examined from early subadults to mature spiders. Serial paraffin sections of the early subadults definitely show that a pair of longitudinal furrows, presumptive lumina of the ovaries, lined with loose cell layers, penetrate perpendicularly into the ovarian tissue. So the basic architecture of the ovary in *N. clavata* is primarily flat cisterna.

Im Falle von reifen Weibchen von *Nephila clavata* setzen sich die Ovarien aus flachen Beuteln zusammen. Um herauszufinden, ob diese strukturelle Fläche angeboren ist oder durch den Druck der reifen Eiern gebildet wird, wurde die Entwicklung der Ovarien vom frühen Subadult bis zum reifen Adult untersucht. In den seriellen Paraffinstückchen vom frühen Subadult zeigte sich, daß ein Paar longitudinale Furchen, die mit zerstreuten Zellenschichten verstärkt wurden, d.h. die präsumptive Lumen, perpendiklar in die Ovariumgewebe gehen. Daraus kann man schließen, daß die Grundarchitektur von diesen Ovarien angeboren aus flachen Beuteln besteht. □*Spider, Nephila, ovary, histology.*

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The golden silk spider, *Nephila clavata* L. Koch, is able to deposit egg masses twice (Kondo, 1988; Shimojana, 1971). Prior to the first oviposition, gravid females possess complicated ovaries whose lumina are expanded among mature eggs. After the second oviposition, the ovarian lumen of exhausted females is not closed and contains immature oocytes and yolk granule debris. In both cases, the basic architecture of the ovary is not clearly identified. In vigorous females immediately after first oviposition, the lumen of the ovary is completely closed and the ovarian epithelium protrudes many young oocytes into the body cavity. In this case the ovarian tubes elongate dorsally and ventrally to form flat cisternae, as if the lumina have been squeezed between mature eggs, already ovulated at the first oviposition, side by side (Kondo and Chaki, 1991).

Generally, however, the spiders have a pair of tubular ovaries or ring-like ovaries. The present study tries to clarify whether the cisternal architecture of the ovary of *N. clavata* is primarily or secondarily formed by pressure from mature eggs.

MATERIALS AND METHODS

Four female subadult and two adult *Nephila clavata* were collected in Funabashi, Central Japan, from late August to early September.

After removal of the cuticle, the entire body or the opisthosoma was fixed in FAA (formalin 5, ethanol 15, glacial acetic acid 1) for 5-21 hours, dehydrated in graded strength of ethanol, embedded in paraffin and sectioned at 6-10μm. Before sectioning, a cut surface of the sample containing mature eggs was treated with distilled water (Kondo, 1969). Serial paraffin sections were stained with Mayer's acid-haemalaum and eosin.

RESULTS

SUBADULTS

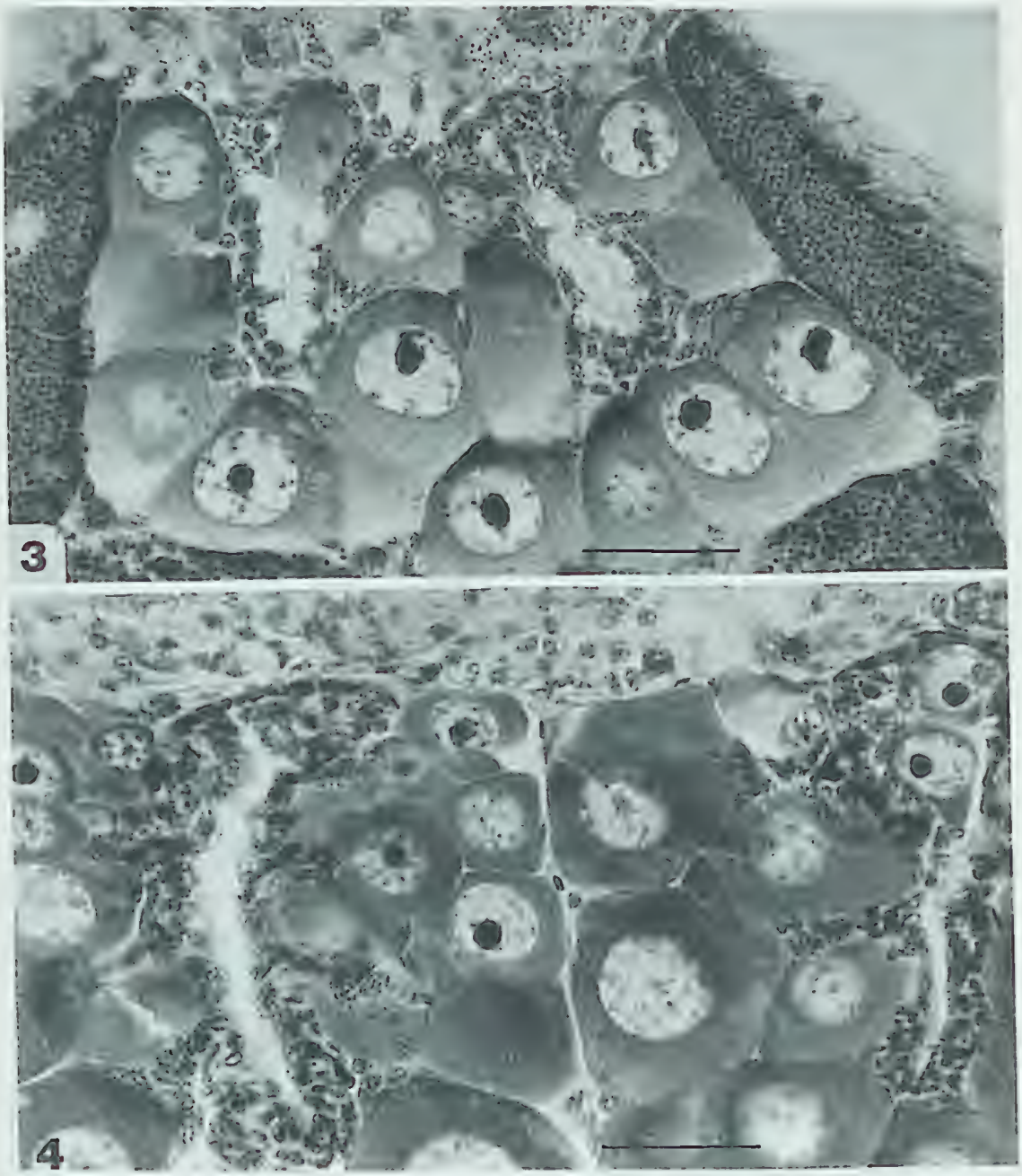
A pair of ovaries was situated behind the book lung extending to the cloacal sac and surrounded by the midgut glands dorsally and by silk glands laterally and ventrally (Figs 1, 2). Although the ovarian tissue was divided in two at the anterior and posterior ends, the left and right ovaries were not separated from each other and formed single rod-shaped tissue for the most part.

Maximum width and thickness of the ovarian tissue were 250μm and 150μm in a small subadult with cephalothorax 1.6 mm wide, 2.6 mm long, and 500μm and 220μm in a large subadult

FIGS 1, 2. 1. Longitudinal section of a large subadult.cs: cloacal sac, m: midgut, mg: midgut gland, ov: ovary, sg: silk gland. 2. Transversal section of a female immediately after final moulting. m: midgut, mg: midgut gland, ov:ovary, sg: silk gland. Scales: 0.5 mm.

whose cephalothorax was 2.8 mm and 4.2 mm respectively.

In transverse sections the ovarian tissue was trapezoidal. In a small subadult, two furrows lined with a loose cell layer penetrated from the upper side of the trapezoid into the ovarian tissue (Fig. 3). The loose cell layer may be the ovarian wall or the ovarian epithelium. Then the furrows seemed to be surrounded by a single layer of the oocytes. Most oocytes, whose cytoplasm was strongly basophilic, were cuboidal or polygonal and 40-50μm in diameter.

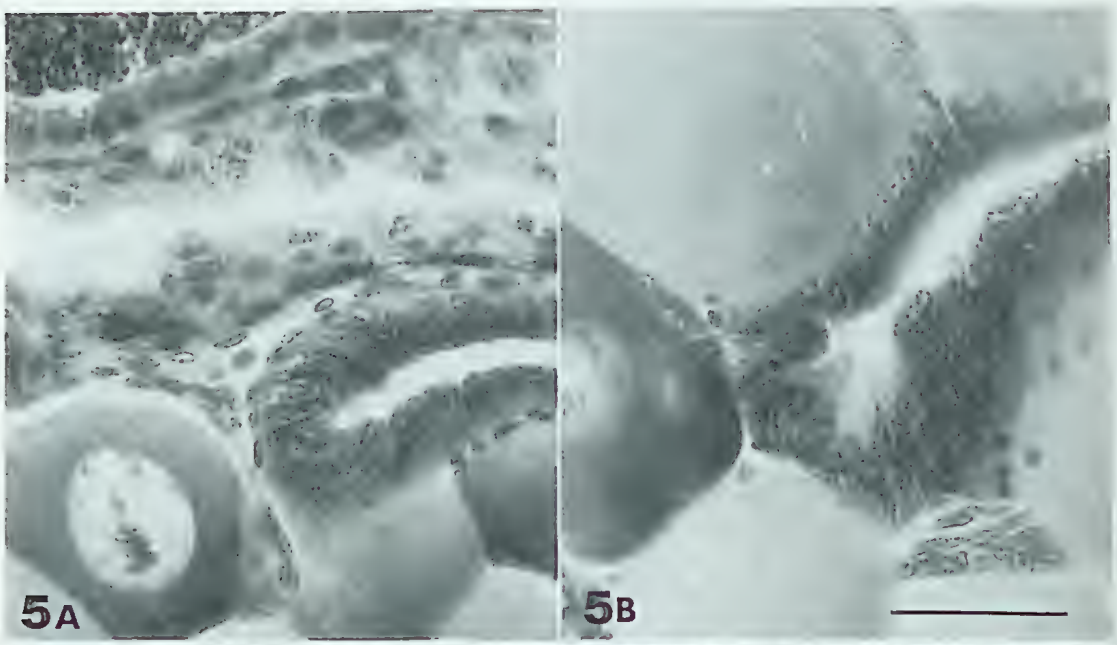


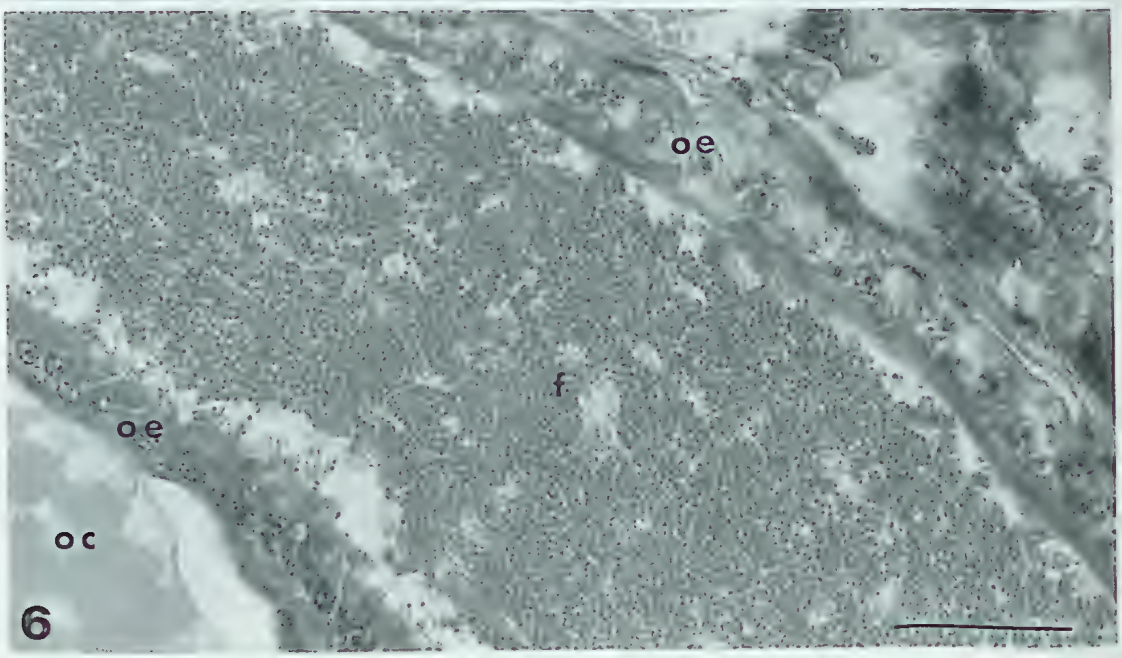
FIGS 3, 4. Transverse section of ovarian tissue in small subadult (3) and in large subadult (4). Scales: 50μm.

The spherical germinal vesicle was 25-35μm in diameter and contained an extremely basophilic and slightly eosinophilic nucleolus. Yolk granules had not formed. The vitelline body or Balbiani's yolk nucleus was not observed.

Each oocyte was connected with the ovarian wall through a short egg stalk or the funiculus. The cells constituting the ovarian wall were more or less columnar and had ellipsoidal nuclei in the basal part and vacuolated protoplasm in the distal part facing the presumptive lumen of the ovary.

In the large subadult, profiles of the oocytes closely resembled the oocytes in the small subadult, though they increased slightly in number





FIGS 5, 6. 5. Transverse section of ovary in female immediately after final moulting. A. Median dorsal part of ovary. B. Distal part of F-shaped lumen of ovary. 6. Lumen of ovary filled with eosinophilic fine granules in a gravid female. f: eosinophilic fine granules, oc: oocyte, oe: ovarian epithelium. Scales: 50µm.

and volume (Fig. 4). A prominent feature was the appearance of narrow lumina in the ovaries, while vacuolate cells in the ovarian wall remained in depth at both the anterior and posterior ends of the ovarian tissue.

ADULTS

In an adult presumably immediately after its final moult, the width of the entire ovaries was approximately 1.0 mm and the lumen of the ovary was F- or T-shaped, branching laterally (Fig. 2). The left and right ovarian epithelia were not

fused, but connected with the oviducts. Total number of oocytes counted in one female was 1,390 including the small oocytes. No oocytes were observed above the dorsal side of the horizontally developing lumina.

Oocytes reached a diameter of 170μm. Germinal vesicles were 40-60μm in diameter. The nucleolus was collapsed and dispersed into nucleoplasm. Cytoplasm of the oocyte was less basophilic (Fig. 2). The eosinophilic yolk granules were neither formed nor accumulated. The ovarian wall seemed to be a simple columnar or pseudostratified epithelium composed of slender, compactly arranged and extremely basophilic cells. Flat cells were lined up between the ovarian epithelium and the oocytes (Fig. 5).

In a gravid female whose ovaries reached 4.0 mm in width, the ovary contained many developing oocytes 380-460μm in diameter, and few immature oocytes. The developing oocytes were filled with eosinophilic yolk granules and had a germinal vesicle 50-60μm in diameter. The lumen of the ovary branches among the developing oocytes. The lumen of the ovary contained eosinophilic fine granules which were presumably a kind of cement substance used to hold the egg mass after oviposition (Fig. 6).

DISCUSSION

The formation of the ovary in *Nephila clavata* was examined from the early subadult stage. The small subadult employed was possibly a nymph of the 6th or 7th instar prior to the penultimate moult. In any case, at an early stage, the longitudinal ovarian walls arise as loose cell layers penetrating from the dorsal side of the ovarian tissue perpendicularly into the mass of the oocytes. The epithelial cells are vacuolated in their distal part and form a lumen which is I-shaped in transverse section. Then, the ovarian epithelium constructs flat rather than cylindrical cisternae.

By the final moult the lumina have been formed in the vacuolated portion of the ovarian epithelium. Immediately after the final moulting, while the oocytes increase in number and volume, a few branches of the lumen arise, mostly in the posterior half of the ovary, forming F- or T-shaped profiles in transverse sections. Simultaneously the oocytes grow and become less basophilic, perhaps due to a cytoplasmic increase. The loose cell layer in the small subadult transforms gradually into columnar epithelium composed of slender, compact and strongly basophilic cells by the final moult. Since the oocytes are connected with this epithelium through egg stalks, it seems to be the ovarian epithelium in the strict sense, though flat cells are aligned along the outside of this epithelium.

Subsequently the oocytes begin vitellogenesis and accumulate eosinophilic yolk granules in their cytoplasm. The lumina of the ovaries continues to branch amongst the oocytes and on the surface of the mass of the oocytes, and they are filled with eosinophilic fine granules which correspond to fine granules attaching to the surface of the chorion of the lycosid egg (Kondo, 1969), the spheres on the chorion (Humphreys, 1983, 1987) or cement substance of the egg mass (Kondo and Chaki, 1991).

In *N. clavata*, the ovarian epithelia of the left and right ovaries are not directly connected with each other, though in archaeid spiders they are connected through a bridge in the posterior portion of the ovaries to form a H-shaped organ (Traciuc and Legendre, 1970). Interstitial tissue, however, does not exist between the left and right ovaries, so the ovaries of *N. clavata* form a single rod-shaped organ. This rod-shaped structure was confirmed not only from both transverse and horizontal sections but also by dissection of the opisthosoma.

In conclusion, in *N. clavata* the basic architecture of the ovary is primarily composed of flat cisterna.

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NEW PREY RECORDS FOR SPIDER HUNTING WASPS (HYMENOPTERA: POMPILIDAE) FROM THE NETHERLANDS

P. KOOMEN AND T.M.J. PEETERS

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In the southern Netherlands, 56 spider prey were collected, and identified, together with their pompilid predators. Those data are compared with data from the literature for northwestern Europe. *Anoplius* spp. seem to prey mainly upon ground dwelling spiders. A strong preference for the wolf spider *Trochosa terricola* was found for *Anoplius viaticus*, in agreement with data from Bristowe (1948). *Episyron rufipes* and *Caliadurgus fasciatellus* attack only orbweb building spiders. Data for *Auplopus carbonarius* and *Dipogon subintermedius* suggest that these species prefer to hunt on vertical planes like tree-trunks. *Arachnospila rufa*, *Pompilus cinereus*, and *Priocnemis* spp. appear to be non-selective.

Dans le sud des Pays-Bas, 56 araignées, proies de Pompilides, on été récoltées avec leurs prédateurs et identifiées. Les données acquises ont été comparées avec les celles de la littérature concernant les observations réalisées aux Pays-Bas et dans les pays voisins. *Anoplius* spp. montre une nette prédilection pour les araignées terricoles. Conformément aux données de Bristowe (1948), *Anoplius viaticus* préfère de loin *Trochosa terricola*. *Episyron rufipes* et *Caliadurgus fasciatellus* s'attaquent seulement aux araignées qui construisent des toiles orbiculaires. Les observations sur *Auplopus carbonarius* et *Dipogon subintermedius* suggèrent que ces espèces chassent de préférence sur des plans verticaux comme des vieux murs ou des troncs d'arbres. *Arachnospila rufa*, *Pompilus cinereus* et les *Priocnemis* spp. semblent être des espèces non sélectives. □*Araneae, predation, Pompilidae, selectivity, The Netherlands.*

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Female Pompilidae attack and paralyse spiders with their sting. Each captured spider is the food of a larva that hatches from an egg laid on the spider. Before oviposition, most European pompilids transport their prey to burrows excavated in the soil, or to pre-existing cavities, e.g., behind bark or between stones (Gauld & Bolton, 1988). Knowledge of pompilid prey is limited for obvious reasons: most hymenopterists are interested only in pompilids and not so much in their prey. Arachnologists tend to accept prey of Pompilidae gratefully, but without identifying their predators. As a consequence, data on prey hardly exist, are out of date and/or are unreliable because of changed taxonomic views, or do not go beyond generic level (e.g., Day, 1988; Oehlke and Wolf, 1987). However, collectively, all published data suggest some prey specialization, but it is not clear if this is due simply to opportunistic behaviour of pompilids, catching only (or mainly) the most abundant prey. A way to gather more knowledge concerning possible preferences of pompilids, is to catch pompilid predators *with* their prey, and to accurately identify them both. Autecological information on the spiders may give a clue as to whether pompilid species only catch what they can, or prefer, for some reason, some species of prey over others. This paper reports on the first results of such a study which began in 1987.

METHODS AND MATERIALS

Pompilids were studied at several locations, mainly in the southern Netherlands, near of Tilburg. Unless stated otherwise, the second author located pompilids by eye and intercepted prey-transporting females using glass tubes and an insect-net. Prey were collected and preserved in alcohol. Predators were collected only if identification in the field was not possible. Wasps were identified with the aid of Wolf (1972), Day (1988) and Oehlke and Wolf (1987). Identification of spiders was based mainly on Roberts (1985ab, 1987). Not all spiders could be identified to species level, because some were juvenile, thus lacking the genital organs necessary for a proper identification. Autecological data on spiders are derived from Jones (1983) and Maurer and Hänggi (1990). All spiders and wasps collected will be lodged in the National Museum of Natural History, Leiden, The Netherlands.

RESULTS

In total, 56 pompilid prey were collected. Data are summarized below. For each specimen the specific date and collecting site are given because both may have influenced hunting behaviour of the wasps. When more than one prey record is available for a single pompilid species, common characteristics of the prey are given that may point to a preference of the actual wasp.

POMPILINAE:

Anoplius concinnus (Dahlbom): *Pardosa* sp. (1 juv., Thorn, 13.x.1990); *Trochosa ruricola* (Degeer) (1♂, Thorn, 13.x.1990). Both are wolf spiders, Lycosidae. They were excavated from a, supposedly, single burrow between pebbles in a gravelpit, after a female *A. concinnus* had been observed showing nest building activity.

Anoplius infuscatus (Vander Linden): Lycosidae (1 juv., Moergestel, 30.iv.1988); *Alopecosa accentuata* (Latreille) (1 juv. Nieuw-Bergen, 6.ix.1991). Both are wolf spiders.

Anoplius viaticus (Linnaeus): *Agroeca brunnea* (Blackwall) (1♀, Beegden, 12.v.1991); *Trochosa terricola* Thorell (1♀ excavated, Alphen en Riel, 5.v.1989; 1♀+1♂, do., 3.v.1988; 1♀, 15.iv.1989, Apeldoorn; 7♀, Beegden, 12.v.1991; 1♀, Hilvarenbeek, 1.v.1988; 3♀+1♂, Berkel-Enschot, 5.v.1989; 1♀, Drunen, 9.v.1989; 1♀, Loon op Zand, 12.iv.1991; 1♀ excavated, Moergestel, 24.iv.1989; 2♀, do., 27.iv.1989; 2♀, do., Moergestel; 2♀, do., 5.v.1989; 1♀, do., 29.v.1989; 1♀, do., 23.vi.1989; 10♀+1♂, do., 29.iii.1990); *Pardosa monticola* (Clerck) (1♀, Beegden, 18.v.1989). All three species are ground dwelling spiders.

Arachnospila rufa (Haupt): *Alopecosa fabrilis* (Clerck) (1♂, Nieuw-Bergen, 1.ix.1991).

Auplopus carbonarius (Scopoli): *Haplodrassus* sp. (1 juv. found in a beehive in one of a group of barrel-shaped cells typical of *A. carbonarius* (Grandi, 1961: 75; Wahis, 1949: 99), Baarle-Nassau, 1991); *Clubiona brevipes* Blackwall (1♀, Udenhout, 11.viii.1990). Both are nocturnal hunters often hiding in silk retreats during the day.

Episyron rufipes (Linnaeus): *Larinioides cornutus* (Clerck) (1♀, Helvoirt, 16.viii.1991); *Nuctenea umbratica* (Clerck) (1 juv., Moergestel, 26.vi.1990). Both are orbweb building spiders.

Pompilus cinereus (Fabricius): Lycosidae (1 juv., Moergestel, 4.viii.1987).

PEPSINAE:

Caliadurgus fasciatellus (Spinola): *Agelenatea redii* (Scopoli) (1 juv., Moergestel, 4.x.1989).

Dipogon subintermedius (Magretti): *Segestria senoculata* (Linnaeus) (1♀ found in a cavity in an old pollard-willow (*Salix alba*), Tilburg, 23.vii.1991).

Priocnemis fennica Haupt: *Clubiona terrestris* Westring (1♀, Hilvarenbeek, 29.ix.1990).

Priocnemis minuta (Vander Linden): Gnaphosidae (1 juv., Moergestel, 17.viii.1988).

Priocnemis susterai Haupt: *Drassodes cupreus* (Blackwall) (1♀, Boxtel, 21.v.1988).

DISCUSSION

The new observations can be compared to data from the literature on pompilids in The Netherlands (Benno, 1969; Bouwman, 1915ab, 1916; Chrysanthus, 1947; Lefeber and Van Ooijen, 1988; Thijsse, 1907; Walrecht, 1936) and nearby countries (Bristowe, 1948; Day, 1981, 1988; Oehlke and Wolf, 1987; Wahis, 1948, 1955, 1962; Wolf, 1971). A summary with references included is given in Table 1. Comments for each pompilid species follow hereafter.

Anoplius concinnus was found with wolf spiders (Lycosidae) as prey. This is in agreement with the literature, where several genera of Lycosidae are mentioned.

Both in The Netherlands and in other countries, a preference for wolf spiders has been recorded for *Anoplius infuscatus*. Beside these, Thomisidae and Agelenidae are mentioned. Most members of these families are 'sit-and-wait' predators, but there are some exceptions, for instance *Thanatus* species and the males of *Textrix* species. So, the available data may point to a preference for ground dwelling spiders.

Anoplius viaticus appeared to prey almost exclusively on the wolf spider *Trochosa terricola* (Lycosidae). These observations are neither restricted to one locality, nor to a short period. Only in two of 41 cases (5%), *A. viaticus* caught other species: *Pardosa monticola* (Lycosidae) and *Agroeca brunnea* (Clubionidae). This suggests that *A. viaticus* did not simply catch the most abundant wandering spider, but rather searched actively for *T. terricola*. In literature on The Netherlands, the *Lycosa* sp. mentioned by Thijsse (1907) might refer to almost any modern lycosid genus. From data on prey elsewhere, the list given by Bristowe (1948) matches our data very well: he found in only seven of 47 cases (15%) prey that were not *Trochosa terricola*. However, other papers indicate several families and genera. Some are hunters by day like Lycosidae, while others are nocturnal hunters (*Drassodes*) or inhabitants of sheet webs (*Agelena*). Common attributes of the recorded spider genera are their medium to large size (5-13 mm) and the strata they occupy: on or near ground level. Most also prefer rather dry and/or sandy places as does *A. viaticus* (*Thanatus*, *Aelurillus*, *Pardosa monticola*, *Trochosa terricola*), but this is not true for

Predator	Prey
Anoplius concinnus	**Lycosidae** (D2): *Arctosa* (O&W), *Pardosa* sp. (K&P, L&VO, O&V), *Trochosa ruricola* (K&P)
Anoplius infuscatus	**Thomisidae** (D2): *Thanatus* (O&W). **Lycosidae** (D2, K&P): *Alopecosa accentuata* (K&P), *Arctosa* (O&W), *Pardosa* (O&W), *Pirata* (O&W), *Tricca* (O&W), *Trochosa* (L&VO, O&W), *Xerolycosa* (O&W). **Agelenidae** (D2): *Textrix* (O&W).
Anoplius viaticus	**Gnaphosidae** (D2): *Drassodes* (O&W). **Clubionidae**: *Agroeca brunnea* (K&P). **Thomisidae** (D2): *Thanatus* (O&W). **Salticidae** (D2): *Aelurillus* (O&W). **Lycosidae** (D2, T): *Alopecosa* (O&W: sub *Tarentula*), *A. accentuata* (B: sub *Tarentula a.*), *A. aculeata* (W3), *A. pulverulenta* (B, W2: sub *Tarentula carinata*), *Arctosa* (O&W), *A. perita* (B), *Pardosa* (O&W), *P. hortensis* (W2), *P. monticola* (B, K&P), *Trochosa* (O&W), *T. terricola* (B, K&P, W3). **Pisauridae**: *Pisaura mirabilis* (O&W, W2). **Agelenidae** (D2): *Agelena* (O&W).
Arachnospila rufa	**Gnaphosidae** (D2): *Drassodes* (O&W), *Gnaphosa* (O&W). **Clubionidae** (D2): *Cheiracanthium* (O&W). **Salticidae** (D2): *Aelurillus* (O&W). **Lycosidae** (D2): *Alopecosa* (O&W: sub *Tarentula*), *A. fabrilis* (P&K), *Trochosa* (O&W).
Auplopus carbonarius	**Zoropsidae**: *Zoropsis* (Wo). **Segestriidae** (D2): *Segestria* (Wo). **Gnaphosidae** (D2): *Aphantaulax* (Wo), *Haplodrassus* sp. (K&P). **Clubionidae** (D2): *Cheiracanthium* (Wo), *Clubiona* (Wo), *C. brevipes* (K&P). **Anyphaenidae** (D2). **Thomisidae** (D2): *Philodromus* (Wo). **Salticidae** (D2): *Dendryphantes* (Wo), *Evarcha* (Wo), *Sitticus* (Wo). **Lycosidae** (D2): *Lycosa* (Wo), *Trochosa* (Wo). **Agelenidae** (D2): *Agelena* (Wo). **Tetragnathidae**: *Meta* (Wa).
Episyron rufipes	**Lycosidae** (D2: only some cases). **Tetragnathidae**: *Meta* (D2). **Araneidae**: *Agelenatea redii* (B: sub *Araneus r.*), *Araneus* (D2, O&W), *A. diadematus* (B), *Argiope* (O&W), *Gibbaranea gibbosa* (L&VO: sub *Araneus gibbosus*), *Larinioides cornutus* (B: sub *A. foliata*, K&P), *Nuctenea umbratica* (K&P).
Pompilus cinereus	**Atypidae**: *Atypus* sp. (C). **Zoropsidae**: *Zoropsis* (O&W). **Gnaphosidae** (D1): *Pterotricha* (O&W). **Clubionidae** (D1): *Cheiracanthium* (O&W). **Zoridae** (D1): *Zora* (O&W). **Thomisidae** (D1): *Xysticus* (O&W). **Salticidae**: *Aelurillus* (O&W), *Ballus* (C: not sure). **Lycosidae** (B1, C, D1, K&P): *Alopecosa* (O&W: sub *Tarentula*), *Arctosa* (O&W), *A. perita* (B, B1, D1, D2, L&VO), *Pardosa* (O&W), *Pirata* (O&W), *Trochosa* (O&W), *Xerolycosa* (D1, D2). **Pisauridae** (D1): *Dolomedes* (O&W). **Araneidae**: *Araneus* (O&W).
Caliadurgus fasciatellus	**Tetragnathidae**: *Meta* (D2, O&W), *M. segmentata* (L&VO). **Araneidae**: *Agelenatea redii* (K&P) *Araneus* (D2, O&W), *A. alsine* (B2), *A. diadematus* (Be, B2, W1), *A. quadratus* (W1).
Dipogon subintermedius	**Segestriidae**: *Segestria* (O&W), *S. senoculata* (D2, K&P). **Salticidae**: *Salticus* (O&W).
Priocnemis fennica	**Clubionidae**: *Clubiona terrestris* (K&P). **Lycosidae**: *Pardosa pullata* (D2).
Priocnemis minuta	**Gnaphosidae** (K&P).
Priocnemis susterai	**Gnaphosidae**: *Drassodes* (O&W), *D. cupreus* (K&P).

TABLE 1. Summary of the prey records in the literature for the pompilid species for which this study gives new data. References are abbreviated: B = Bristowe, 1948; Be = Benno, 1969; B1 = Bouwman, 1915b; B2 = Bouwman, 1916; C = Chrysanthus, 1947; D1 = Day, 1981; D2 = Day, 1988; K&P = Koomen & Peeters, this study; L&VO = Lefeber and Van Ooijen, 1988; O&W = Oehlke and Wolf, 1987; T = Thijsse, 1907; Wa = Walrecht, 1936; Wo = Wolf, 1971; W1 = Wahis, 1948; W2 = Wahis, 1955; W3 = Wahis, 1962.

Agroeca brunnea, an inhabitant of wet places. So, although our observations and Bristowe (1948) suggest a strong preference for only one species of Lycosidae, data from other countries show a much broader spectrum of prey. This may point to a preference for *Trochosa terricola*, that is abandoned when the latter species is not available.

Arachnospila rufa is not selective: spiders with various sizes, and from several habitats and strata have been recorded. Our observations support these data.

For *Auplopus carbonarius*, the observations that Segestriidae, *Clubiona brevipes*, Anyphaenidae, and *Dendryphantes* were prey items may point to a preference for spiders that walk along, or hide in crevices in, vertical planes, e.g. walls or tree-trunks. Species with (at least occasionally) similar habits are found in most of the other families and genera recorded (*Zoropsis*, *Aphantaulax*, *Haplodrassus*, *Philodromus*, *Evarcha*, *Sitticus*, *Agelena*, *Meta*), but without species identifications, the hypothesis that *A. carbonarius* is mainly a vertical hunter cannot be supported or falsified. Several authors note that *A. carbonarius* has a habit of amputating the legs of its preys (e.g., Grandi, 1961: fig. 48; Oehlke and Wolf, 1987). This did not occur in the two cases we noted. Both the *Haplodrassus* and the *Clubiona* prey still had all of their legs.

Episyron rufipes was found to prey upon two araneid spiders. Using data from other countries (see Table 1) it can be deduced that *E. rufipes* specializes on orbweb building spiders.

For *Pompilus cinereus* many different prey are known, including burrowing spiders (*Atypus*), orbweb building spiders (*Araneus*), and xerophylic (*Arctosa perita*, *Aelurillus*) and hygrophylic species (*Dolomedes*). This suggests no specificity at all. To date, only one juvenile wolf spider can be added.

Caliadurgus fasciatellus is a second pompilid species that is obviously specialized in capturing orbweb building spiders. The *Araneus redii* prey fits well within these data (Table 1).

The recorded prey of *Dipogon subintermedius*

are in conformity with its observed hunting places: tree-trunks and piles of fences. *Segestria senoculata* is known to build its retreat in these places, and jumping spiders from the genus *Salticus* may also be found there.

For the three species of *Priocnemis*, viz., *P. fennica*, *P. minuta*, and *P. susterai*, reliable data from the literature are few, because formerly these species were not distinguished as separate taxa. Prey recorded so far do not suggest any high degree of selectivity.

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GROUND-LIVING SPIDERS (ARANEAE) ONE YEAR AFTER FIRE IN THREE SUBARCTIC FOREST TYPES, QUÉBEC (CANADA)

SEPPO KOPONEN

Koponen, S. 1993 11 11: Ground-living spiders (Araneae) one year after fire in three subarctic forest types, Québec (Canada). *Memoirs of the Queensland Museum* **33**(2): 575-578. Brisbane. ISSN 0079-8835.

The ground-living spider fauna was studied one year after fire using pitfall traps in three forest types of subarctic Québec, July-August 1990. About 30 species, of the total 47 found at burned sites, were regarded as pioneer or colonizer species. Spiders captured commonly at burned sites included e.g. *Gnaphosa microps* Holm, *G. muscorum* (L. Koch), *Pardosa hyperborea* (Thorell), *P. uintana* Gertsch, *Trochosa terricola* Thorell, *Alopecosa aculeata* (Clerck), *Diplocentria bidentata* (Emerton), and *Sisis rotundus* (Emerton). Some species were found only or predominantly at unburned sites; e.g. *Pardosa moesta* Banks and *Lepthyphantes complicatus* (Emerton).

En juillet-août 1990, une année après des incendies, la faune des araignées habitant sur le sol des trois types de fôret du Québec subarctique a été étudiée en utilisant des pièges-fosses. Environ 30 espèces, d'un total de 47 trouvées dans les sites brûlés, ont été considerées comme des espèces pionnières ou colonisatrices. Les araignées capturées généralement dans les sites brûlés comprennent par exemple *Gnaphosa microps* Holm, *G. muscorum* (L. Koch), *Pardosa hyperborea* (Thorell), *P. uintana* Gertsch, *Trochosa terricola* Thorell, *Alopecosa aculeata* (Clerck), *Diplocentria bidentata* (Emerton), et *Sisis rotundatus* (Emerton). Quelques espèces ont été trouvées seulement ou principalement dans les sites non brûlés, par exemple, *Pardosa moesta* Banks et *Lepthyphantes complicatus* (Emerton). □*Araneae, forest fire, subarctic, Canada.*

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Fire history, effect of fire on forest vegetation, and postfire succession of plant cover have been studied in detail in northern Québec (e.g. Payette *et al.*, 1989). By contrast, very little is known about the effects of fire on spiders in northern forests of North America. In central Alaska, Beckwith and Werner (1979) suggested that the decrease of many arthropod populations after fire can be attributed to increasing spider populations and predation by spiders. Data from temperate forests of North America are also markedly scant (e.g. Pearse, 1943; Buffington, 1967). Pearse (1943) listed about 35 species of spiders from burned pine forests in North Carolina; however, individual numbers were low.

In forests of northern Europe, postfire spider faunas and their succession have been studied both after natural fires and prescribed burning (e.g. Huhta, 1971; Schaefer, 1980; Hauge and Kvamme, 1983; Koponen, 1988, 1989). Data from subarctic forests of Europe are available only from northern Finland (Huhta, 1971; Koponen, 1988, 1989).

This paper deals with the effects of fire on ground-living spiders at the beginning of faunal succession in three forest types in the subarctic zone of Québec, Canada. Forest fires occurred in midsummer 1989; samples were collected in 1990 during the first postfire summer.

MATERIALS AND METHODS

The study areas were situated 1) at Lac Ekomiak (53°23'N, 77°30'W), south of La Grande/Radisson and 2) at Kuujjuarapik (Poste-de-la-Baleine; 55°17'N, 77°48'W) on the eastern coast of Hudson Bay (Fig. 1). Both study areas were near the northern limits of the boreal forest.

1. At Lac Ekomiak, large areas of forest (thousands of sq. km) were burned in midsummer 1989. The study sites situated near the border of this extensive fire area were in dry and mesic forest. The main tree species were *Pinus banksiana* Lamb. and *Picea mariana* (Mill.) B.S.B. at dry sites; *Picea mariana* and *Larix laricina* (Du Roi) K. Koch at mesic sites. The ground layer of the dry sites was characterized by *Cladonia* and *Pleurozium*; that of the mesic sites by *Sphagnum* and *Pleurozium*. The fire had been very intensive and had killed all trees and destroyed field and ground layer vegetation totally. The trapping

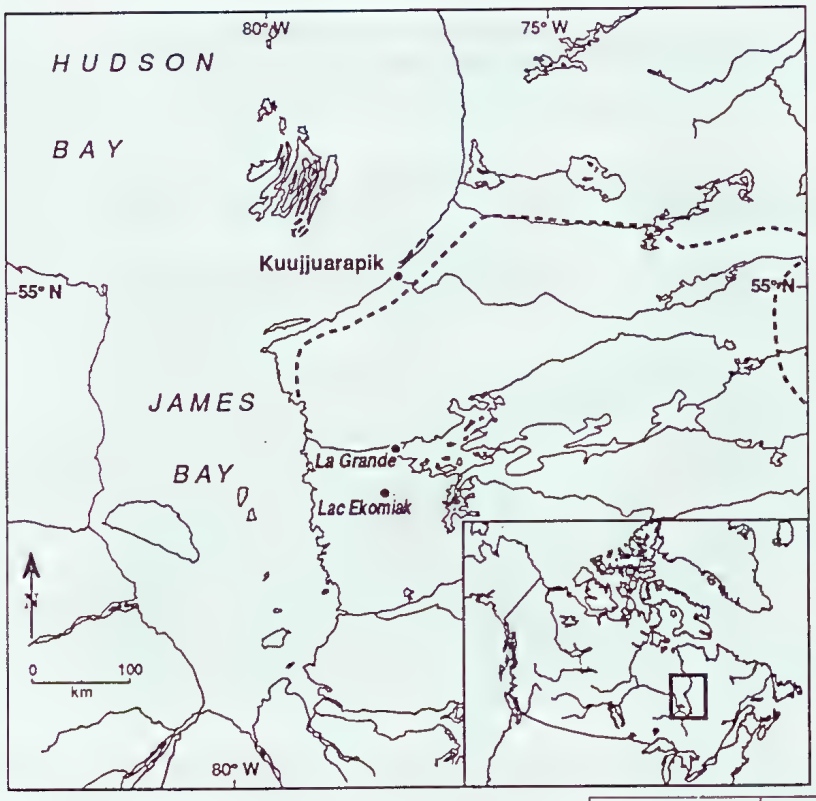

FIG. 1 (left). Postfire study sites at Lac Ekomiak and Kuujjuarapik, Québec. Broken line indicates the northern limit of the continuous (subarctic) forest.

TABLE 1 (right). Total number of individuals in major spider families, total number of species, diversity (H) and evenness (E) for pitfall trap material at Lac Ekomiak and Kuujjuarapik, Québec. LDB = Lac Ekomiak dry burned, LDC = Lac Ekomiak dry unburned, LMB = Lac Ekomiak mesic burned, LMC = Lac Ekomiak mesic unburned, KB = Kuujjuarapik burned, KC = Kuujjuarapik unburned site

	LDB	LDC	LMB	LMC	KB	KC
Lycosidae, inds.	59	16	45	32	104	28
Linyphiidae, inds.	44	35	34	22	110	172
Gnaphosidae, inds.	6	8	6	3	11	3
Others, inds.	6	5	6	14	3	0
Total, inds.	115	64	91	71	228	203
Species richness	24	13	15	18	31	20
Shannon H	3.98	3.27	3.50	3.52	3.62	3.31
Evenness E	0.87	0.88	0.90	0.84	0.73	0.77

period was 24 July-20 August 1990; traps were not changed during the period.

2. At Kuujjuarapik, a small area (about 50 x 15m) of *Picea glauca* (Moench) Voss forest was burned in July 1989. The site is in an isolated, small-sized woodland near forestline. Ground layer was dominated by *Pleurozium* and *Empetrum*. The field and ground layer vegetation was destroyed but the intensity of fire had been less than at Lac Ekomiak. The trapping period was 14 July-19 August 1990. The traps were changed once (1 August).

Ten traps were placed at each site (dry burned, dry unburned, mesic burned and mesic unburned) at Lac Ekomiak and five traps at each site (burned and unburned) at Kuujjuarapik. Pitfall traps were plastic cups (diameter 6.5cm, height 7cm) with ethylene glycol (2.5cm) as a preservation liquid. They were provided with covers (12 x 12cm) against rainfall and litter, and there was 2-3cm space between the cover and the ground. Traps were placed in a line at each site, average distance between the traps being 2m.

The indices used are Shannon-Wiener index of diversity:

$$H = -\sum_{i=1}^{s}(p_i)(log_2\, p_i)$$

and evenness: E = H/logS (S = number of species, p_i = proportion of total sample belonging to the ith species). The spider material is deposited in the Zoological Museum, University of Turku, Finland.

	Species	n	%BS	site 'preference'
DRY SITE	*Alopecosa aculeata*	6	100.0	only at burned
	Pardosa hyperborea	15	93.3	strongly to burned
	Diplocentria bidentata	10	90.0	strongly to burned
	Trochosa terricola	16	75.0	to burned
	Pardosa spp.*	31	58.1	equally occurring
	Gnaphosa spp.	8	50.0	equally occurring
	Agyneta olivacea	7	42.9	equally occurring
	*Hilaira herniosa***	13	15.4	to control
MESIC SITE	*Pardosa hyperborea*	10	90.0	strongly to burned
	Diplocentria bidentata	6	83.3	to burned
	Gnaphosa microps	9	66.7	slightly to burned
	Pardosa spp.*	42	66.7	slightly to burned
	Ozyptila gertschi	13	46.2	equally occurring
	*Hilaira herniosa***	7	14.3	to control
	Pardosa moesta	15	0.0	only at control

TABLE 2. Common spiders (≥ 6) trapped at burned and unburned (control) sites, at Lac Ekomiak, Québec. n = total number of individuals trapped, both sites combined; %BS= percentage individuals caught at burned site . * = *Pardosa uintana, P. mackenziana* and *P. xerampelina*; ** = adults of *H. herniosa* and juvenile *Hilaira* specimens.

Species	n	% BS	'preference'
Pardosa hyperborea	16	100.0	only at burned site
Pocadicnemis americana	6	100.0	only at burned site
Arctosa alpigena	9	77.8	to burned site
Pardosa uintana	100	74.0	to burned site
Gnaphosa muscorum	10	70.0	slightly to burned site
Sisis rotundus	10	60.0	equally occurring
Sisicottus montanus	22	59.1	equally occurring
Agyneta allosubtilis	19	15.8	to control site
Latithorax obtusus	13	15.4	to control site
Lepthyphantes alpinus	7	14.3	to control site
*Hilaira herniosa**	66	13.6	to control site
Lepthyphantes complicatus	19	5.3	strongly to control site

TABLE 3. Common spiders (≥ 6) trapped at burned and unburned (control) sites at Kuujjuarapik, Québec. n = total no. of individuals trapped, both sites combined; % BS =percentage individuals caught at burned site; * = adults of *H. herniosa* and juvenile *Hilaira* specimens.

RESULTS

A total of 772 spiders was collected from 6 study sites (3 burned, 3 unburned) in northern Québec during July-August, 1990. Individuals of two families, Linyphiidae and Lycosidae, clearly dominated all collections; individuals of Gnaphosidae ranked third among trap captures (Table 1).

Both at Lac Ekomiak and at Kuujjuarapik, trap captures were higher at burned sites than at unburned sites. This was mainly due to the great numbers of Lycosidae caught at open burned sites. The figures for the two most abundant families were (Lac Ekomiak and Kuujjuarapik combined): Lycosidae 208 at burned and 76 at unburned sites, Linyphiidae 188 and 229 respectively. In general, at the burned sites, the diversity (H) was higher or equal compared to the unburned controls (Table 1).

Altogether 56 species were caught, 37 species were trapped at Lac Ekomiak and 34 at Kuujjuarapik. Number of species from burned sites was 47; from unburned sites 37; 28 species were common to both burned and unburned sites. Linyphiidae (Erigoninae and Linyphiinae), Lycosidae, and Gnaphosidae were numerically dominant in species number, with 31 (24 and 7), 9 and 6 respectively.

Species that actively colonized the burned sites included, among the lycosids, *Pardosa hyperborea* (Thorell) in both study areas and *Alopecosa aculeata* (Clerck) at Lac Ekomiak (Tables 2, 3). The species group of *Pardosa uintana* Gertsch, *P. mackenziana* (Keyserling) and *P. xerampelina* (Keyserling), including many juveniles, as well as *Arctosa alpigena* (Doleschal) at Kuujjuarapik, and *Trochosa terricola* Thorell at Lac Ekomiak, also were more abundant at burned than unburned sites.

The gnaphosids caught, *Gnaphosa microps* Holm and *G. muscorum* (L.Koch), were slightly more abundant at burned than unburned sites. Of the linyphiids (Erigoninae), *Diplocentria bidentata* (Emerton) and *Pocadicnemis americana* Millidge apparently 'preferred' burnt areas (Tables 2, 3).

Many species were represented by less than 6 individuals captured, and consequently not included in the Tables 2, 3. Several were found only at burned sites. This group included: *Gnaphosa parvula* Banks, *Zelotes fratris* Chamberlin, *Pardosa furcifera* (Thorell), *Neon nelli* Peckham and Peckham, *Sisicus apertus* (Holm), *Ceraticelus atriceps* (O.P.-Cambridge), *Horcotes quadricristatus* (Emerton), *Sciastes truncatus* (Emerton), *Tunagyna debilis* (Banks), *Walckenaeria atrotibialis* O.P.-Cambridge, *W. castanea* (Emerton), *W. directa* (O.P.-Cambridge) and *W. tricornis* (Emerton).

Several species seemed to lack habitat specificity and were equally found in marked numbers at both burned and unburned sites. Such species included the linyphiids, *Sisis rotundus*

(Emerton), *Sisicottus montanus* (Emerton) and *Agyneta olivacea* (Emerton); and the thomisid *Ozyptila gertschi* Kurata. These generalist species must be regarded as colonizer species because of their common occurrence at burned sites. Although only in a few cases (*Pardosa hyperborea* and *P. uintana*) 'preferences' to burned areas were statistically significant, about 30 of the 47 species caught at burned sites can be regarded as potential colonizers in the subarctic postfire forests investigated.

Species that clearly avoided burned sites were the linyphiids *Lepthyphantes complicatus* (Emerton), *L. alpinus* (Emerton), *Hilaira herniosa* (Thorell), *Latithorax obtusus* (Emerton), and *Agyneta allosubtilis* Loksa. Of the lycosids, *Pardosa moesta* Banks was found only at the unburned mesic forest at Lac Ekomiak.

DISCUSSION

The burned areas at Lac Ekomiak and at Kuujjuarapik greatly differed both in the intensity of fire and in the size of area burned. At Kuujjuarapik, spiders easily colonized the burned site from surrounding nearby natural areas. By contrast, at Lac Ekomiak, species colonizing the burned sites came from long distances (i.e., several hundred metres), especially at the dry burned site. The possible survival of spiders in the burnt area during the fire is open to discussion (cf. McKay, 1979: 246); however, at the dry burned site its seems to be improbable due to the intensity of the fire.

The spider community trapped at burned sites one year after fire was rich; the diversity (H) was not lower than at unburned sites. Similar results were found in subarctic Finland during the first postfire summer (Koponen, 1988). This contrasts with some earlier studies (Schaefer, 1980; Metz and Dindal, 1980). However, also Schaefer (1980) observed high diversity values already two years after fire in pine forests of Germany.

Some of the species that colonized burned sites in northern Québec are considered pioneer species in other northern areas, e.g. *Diplocentria bidentata* in burned areas of northern Finland (Koponen, 1988).

ACKNOWLEDGEMENTS

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DIVERGENT TRANSFORMATION OF CHELICERAE AND ORIGINAL ARRANGEMENT OF EYES IN SPIDERS (ARACHNIDA, ARANEAE)

OTTO KRAUS AND MARGARETE KRAUS

Kraus, O. and Kraus, M. 1993 11 11: Divergent transformation of chelicerae and original arrangement of eyes in spiders (Arachnida, Araneae). *Memoirs of the Queensland Museum* 33(2): 579-584. Brisbane. ISSN 0079-8835.

In various higher taxa of the Araneae (e.g., Mesothelae, Migidae, Hypochilidae), the chelicerae and their fangs show an intermediate position between those commonly called orthognathy and labidognathy. This stage is considered to form part of the ground pattern of spiders; accordingly, it is called plagiognathy (new term). It is concluded that plagiognathy gave rise to orthognathy and labidognathy as divergent adaptational developments. In most instances, plagiognathy is correlated with the maintenance of the original (plesiomorphous) arrangement of the lateral eyes (= ALE + PLE + PME) in triads or semi-triads. The previous assumption that orthognathy and the arrangement of eight eyes in two subparallel rows are characters that were already present in ancestral spiders is refuted.

Bei verschiedenen höheren Taxa der Araneae (z.B. Mesothelae, Migidae, Hypochilidae) weisen die Cheliceren sowie deren Klauen eine intermediäre Position zwischen Orthognathie und Labidognathie im üblichen Sinne auf. Diese Anordnung wird als Teil des Grundmusters der Echten Spinnen angesehen und hierfür die neue Bezeichnung Plagiognathie eingeführt. Von diesem primären plagiognathen Zustand werden sowohl die Orthognathie als auch die Labidognathie als divergente Entwicklungen mit unterschiedlichem Anpassungswert abgeleitet. In den meisten Fällen ist Plagiognathie korreliert mit dem Erhalt der ursprünglichen (plesiomorphen) Anordnung der Seitenaugen (VSA + HSA + HMA) in Form von Triaden oder Semi-Triaden. Die bisherige Annahme ist nicht länger aufrecht zu erhalten, wonach Orthognathie und die Anordnung von 8 Augen in zwei Querreihen als Komponenten des Grundmusters der Spinnen angesehen worden waren. □*Araneae, plagiognathy, orthognathy, labidognathy, lateral eyes, triads.*

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It is generally believed that the chelicerae in spiders can be arranged in either of two different ways, described by the terms orthognathy and labidognathy. Orthognathy is commonly thought to represent the primitive (plesiomorphic) character stage (Foelix, 1982: 3; Platnick and Gertsch, 1976: 13). At first glance, this view seems to be supported by the fact that a strictly orthognathous arrangement of these mouthparts is also present in the outgroup of the Araneae, i.e., in the Amblypygi. Hence, the idea that orthognathy is a plesiomorphic feature seems to be the most parsimonious explanation. Accordingly, labidognathy is regarded as a derived (apomorphic) feature. Kaestner (e.g., 1952, 1953a, b) presented arguments supporting the assumption that labidognathous, i.e., cooperating chelicerae had various functional advantages. He produced a model (Fig. 1) illustrating the transformation of a 'primitive' orthognathous arrangement into the labidognathous position. However, it is difficult to imagine how this could have happened gradually, and Kaestner did not explain why orthognathy had been maintained in a considerable number of higher taxa.

Simon (1892: 64, 82) pointed out that the Liphistiidae and Migidae had arrangements of the chelicerae that did not fit very well into the generally accepted orthognathy/labidognathy scheme. Later authors ignored such 'deviations', however, and continued to base the distinction of two major subtaxa of spiders–Mygalomorphae (=Orthognatha) and Araneomorphae (=Labidognatha) on different positions of the chelicerae. Kaestner alone remarked on the intermediate arrangement of these mouthparts in Actinopodidae and in *Hypochilus*, but apparently he too continued to adhere to the typological orthognathy/labidognathy concept. One main aspect of his study was therefore to classify the chelicerae in *Hypochilus* as orthognathous *or* labidognathous.

In this paper, we will present relevant facts, most of them already known for decades, and discuss conclusions allowed by alternative concepts.

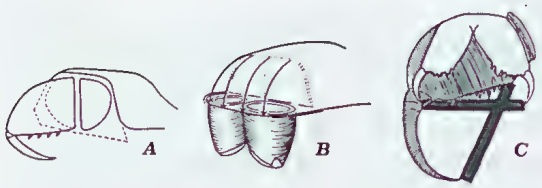

FIG. 1. Transformation of chelicerae as supposed by Kaestner. A, orthognathy, left chelicera omitted, front of prosoma nearly vertical. B, labidognathy, dotted lines and arrows indicate how front of prosoma (with chelicerae) shifted from original vertical to a horizontal position (rotation of basal segments of chelicerae not indicated). C, suggested economy of relatively small cooperating labidognathous chelicerae compared with a single orthognathous chelicera (hatched); both seize objects of same size.–(From Kaestner, 1953b).

This approach leads directly into a critical discussion of another generally accepted dogma in arachnology—that the eight eyes present in the ground pattern in spiders were originally arranged in two more or less parallel rows. In the nearest outgroups (Amblypygi, Uropygi), however, the arrangement of these eight eyes is quite different: the lateral eyes form triads on both sides of the prosoma. Such triads also occur in certain spiders. We therefore also plan to adopt a somewhat unconventional approach, discussing the question as to whether the presence of such triads in various subtaxa of the Araneae could be a persisting plesiomorphic character expression.

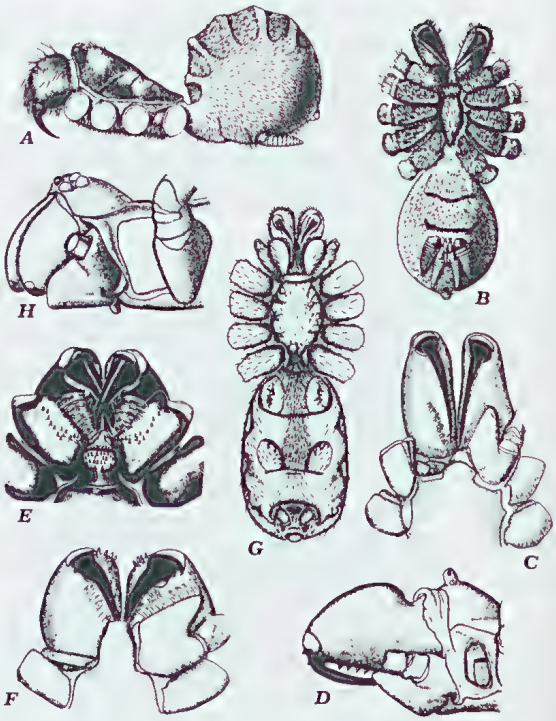

FIG. 2. Position of chelicerae and fangs, lateral and ventral views. A-B, Mesothelae: *Liphistius* sp. C-D, Atypidae: *Atypus affinis*. E, Migidae: *Migas quintus*. F, Actinopodidae: *Missulena occatoria*. G, Hypochilidae: *Hypochilus gertschi*. H, *H. thorelli*.– (A-B from Millot, 1949; C-D, F, H from Kaestner, 1952; E from Wilton, 1968).

RESULTS AND INTERPRETATIONS

Chelicerae

FACTS.

Orthognathy is commonly regarded as plesiomorphic. However, precisely those spiders that have the greatest number of plesiomorphies in common (Platnick and Gertsch, 1976) do not show an orthognathous position of their chelicerae: in the Liphistiidae (Figs 2a-b) the basal segment (paturon) of these mouthparts is relatively short, inflated and obliquely positioned. Further, the longer axis of this basal segment is orientated obliquely downwards, and not horizontally and paraxially as in 'true' Orthognatha (Figs 2c-d). The corresponding position of the fangs is also oblique, and anything but paraxial, in contrast to the position of the fangs in *Atypus*, for example (see Simon, 1892: 64).

The same situation as in *Liphistius* is also found in various subtaxa of the Mygalomorphae. In 1892, Simon (: 82) described similar arrangements in the Migidae, referring to 'chélicères très courtes, convexes à la base, mais ensuite brusquement inclinées, presque verticalement ...' (see Fig. 2e). Kaestner (1952: 118) studied *Sason robustum* (O. P.-Cambridge, 1883) as a representative of the Barychelidae and characterized the chelicerae as short and subvertically inclined. In the same paper, Kaestner demonstrated that obliquely arranged chelicerae were also present in the Actinopodidae (Fig. 2f); he described the situation in *Missulena occatoria* (Walckenaer, 1805) and concluded: 'I cannot see any biological reason for such conditions. But as torsions of this kind play an important role in the origin of labidognathy, it is interesting to see that they [the torsions] may also occur in the Orthognatha' (transl. from German).

It is worth mentioning that the chelicerae even of the oldest known spider, *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987) (Middle Devonian), had short basal segments and also fangs (Selden *et al.*, 1991, e.g., plate 1, figs 6-8).

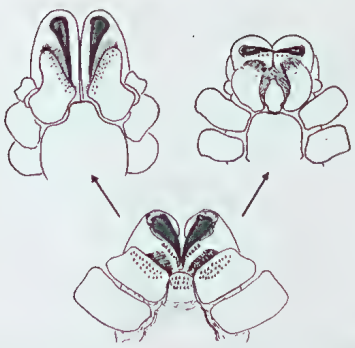

FIG. 3. Orthognathy (left) and labidognathy (right) as apomorphic character states derived from plagiognathy (bottom).

Unfortunately, their original position is unknown.

Chelicerae with an oblique position are also found in a taxon that unquestionably belongs to the Araneomorphae (= Labidognatha *auct.*): the Hypochilidae (Figs 2g-h). Again, it was Kaestner (1952: 132) who studied details. He concluded that the mouthparts in *Hypochilus* were of the orthognathous type in construction and expressed the view (Kaestner, 1952: 114) that 'the majority of important characters present in *Hypochilus* is in accordance with the Orthognatha, whereas the number of features present in Labidognatha only is very low. For this reason, I must remove the genus from the suborder Labidognatha and either place it in the Orthognatha or set it up in a suborder of its own' (transl. from German).

INTERPRETATION

Kaestner maintained that labidognathy was an advanced character state, which had developed from an orthognathous ground pattern by gradual transformation (Kaestner, 1953a: 60; Fig. 1). He felt that *Hypochilus* (and the Hypochilidae) should be regarded as transitory stages and explained the oblique position also present in the Barychelidae and Actinopodidae as a parallel development. Furthermore, he regarded the 'semi-orthognathous' chelicerae in *Dysdera* (Dysderidae) as intermediate. Kaestner thought, then, that various transitory stages still existed, forming a 'phylogenetic link' between the two extreme character states.

We reject this judgement based on typology, and postulate that an oblique position of the chelicerae, including the fangs, really represents the plesiomorphic situation (Fig. 3). As a new term is needed, we would like to suggest 'plagiognathy' to designate this original position of the chelicerae. Accordingly, the plagiognathous position present in the ground pattern of the Araneae has been secondarily transformed in two different directions, both apomorphic character states: orthognathy and labidognathy (Fig. 3). We see various arguments in support of this hypothesis:

a) It explains why orthognathy is not encountered in the Mesothelae (*Liphistius*, *Heptathela*).

b) The absence of orthognathy in representatives of several mygalomorph families is explained.

c) The fact that the Hypochilidae are not labidognathous is explained by the simple assumption that the original plagiognathy has been maintained in this group of the Araneomorphae. Nonetheless, in all other Araneomorphae (this means in the Neocribellatae, the sister taxon to the Hypochilidae) labidognathy has been achieved and is regarded as an apomorphy of this taxon. This conclusion is not invalidated by the fact that superficially orthognathous arrangements originated secondarily in a few sexually dimorphic araneomorph taxa (e.g., in males of the salticid genus *Myrmarachne*).

d) Kaestner's typological and entirely theoretical model suggesting how a supposed transition from orthognathy to labidognathy could come about (Fig. 1) is replaced by a new concept (Fig. 3). This postulates divergent and gradual evolutionary change of the ground pattern, that is to say, of plagiognathy.

e) Kaestner's complicated assumption that obliquely arranged chelicerae originated in parallel both in the Mygalomorphae and the Araneomorphae is replaced by a simple, comprehensive hypothesis.

The only remaining conflict seems to be that reflected in the strictly orthognathous position of the chelicerae in the most closely related outgroups of the Araneae (Amblypygi, Uropygi). If our 'plagiognathy hypothesis' is correct, it must be assumed that orthognathy in the Araneae is a different and thus independent secondary development within the mygalomorph spiders. There is no question but that this contradiction needs some further examination.

Preliminary investigations have already suggested that orthognathy in Amblypygi may be different from orthognathy in spiders: the basal segment in amblypygid chelicerae has a long, stout apodeme at its proximal dorsolateral border, which reaches deeply into the broad, flat prosoma. This peculiarity is lacking in plagio-

gnathous and also in orthognathous chelicerae of spiders. We expect that more detailed studies on the functional morphology, including the musculature, will demonstrate that orthognathy in uropygids and amblypygids differs from orthognathy in spiders. This would support our view and could perhaps constitute point f) in the list of positive arguments above.

EYES

Surprisingly, plagiognathous spiders (for example Mesothelae, Migidae, Hypochilidae) share a special arrangement of the eyes (Figs 4g, e, c): anterior lateral, posterior lateral and posterior median eyes are grouped closely together. This prompts the following remarks on the question as to how the eyes were grouped in the ground pattern of the Araneae.

As designations widely used in taxonomic descriptions (AME, ALE, PME, PLE) disregard the origin of these 'ocelli', some notes on the homolgy of the eyes of spiders may be appropriate to ensure that we understand each other: the anterior median eyes (AME) will be called 'median eyes' by us, as they are homologous with the median eyes of other arthropods (for example those in Xiphosura, 'ocelli' in insects, and the three components of crustacean nauplius eyes). All other eyes, three on each side, will be called 'lateral eyes' (ALE + PLE + PME), as they are homologous with the paired original compound eyes in arthropods, for example, in xiphosurans.

FACTS

It is commonly believed that an arrangement in two transverse rows of eight eyes is plesiomorphic. Only two weak aspects support this view, however: (a) there is no reason at all to doubt that the presence of eight eyes forms part of the araneid ground pattern, and (b) their arrangement in two rows is widely observed both in the Mygalomorphae (for example the Actinopodidae; see Simon, 1892: 79, figs 81-83) and in the Araneomorpha (for example Araneidae, Eusparassidae, Thomisidae).

On the other hand, lateral eyes more or less distinctly grouped in triads occur in various groups of spiders. Mesothelae, Migidae and Hypochilidae have already been mentioned. Almost perfect triads occur in Pholcidae (Fig. 4f). The same is true of Amblypygi (Fig. 4b) and Uropygi, the direct outgroups to spiders!

The arrangement of the eyes in the extinct Trigonotarbida deserves special attention. According to Selden *et al.* (1991: 254), they form the sister group of all other pulmonate taxa (= Araneae + Amblypygi + Uropygi + Schizomida). Devonian trigonotarbids had the usual two median eyes, and the lateral eyes were represented by up to 9 (12 ?) lenses (Fig. 4a). Three of these were major lenses, while the others were minor lenses arranged in the interspace between the major ones (Shear *et al.*, 1987). This kind of transformation of the original compound eyes clearly indicates that a triad of major lateral eyes is a feature of the ground pattern of the pulmonates as a whole; accordingly, the loss of the minor lateral eyes could be regarded as an autapomorphy of all other pulmonates, including spiders. This secondary reduction of the minor lateral eyes may explain why most triads are not perfectly closed, not even in amblypygids (Fig. 4b).

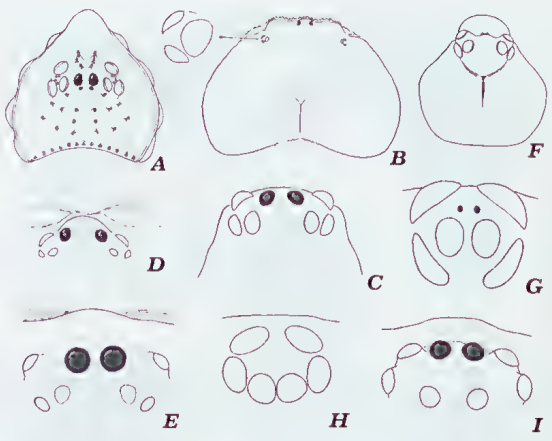

FIG. 4. Position of median (black) and lateral eyes in Trigonotarbida, Amblypygi and Araneae. A, Trigonotarbida: *Gilboarachne grierson*i, reconstruction of prosoma (from Shear *et al.*, 1987). - B, Amblypygi: *Damon* sp. C, Hypochilidae: *Hypochilus gertschi*. D, Atypidae: *Atypus affinis*. E, Migidae: *Poecilomigas* sp. F, Pholcidae: *Pholcus circularis*. G, Mesothelae: *Liphistius* sp. H, Dysderidae: *Dysdera* sp. I, Agelenidae: *Agelena* sp. (Not to scale).

The peculiarity 'lateral eyes in triads' is commonly used as a character in spider identification keys, but as far as we can tell, its potential bearing on phylogeny has never been discussed. Could it be that triads of lateral eyes are part of the ground pattern in the Araneae?

A survey of how the lateral eyes are positioned in representatives of higher taxa of spiders shows that almost perfectly 'closed' triads (as in pholcids) are rare. In most instances, the three lateral eyes on each side are somewhat dissociated. In addition to the Mesothelae and Migidae already mentioned, we should also like to draw attention

to the Atypidae (Fig. 4d) and to the illustrations in Raven's comprehensive study of the Mygalomorphae (1985). In many cases the posterior lateral and the posterior median eyes are closely connected, with some distance between them and the anterior laterals. *Hypochilus* shows slightly dissociated triads (Fig. 4c). The Dysderidae (Fig. 4e) and Oonopidae are six-eyed spiders, having the median eyes completely reduced. In dysderids, the lateral eyes are closely grouped together, resembling the arrangement of the laterals in the Mesothelae. In many groups within the Araneomorphae, diads are present instead of triads. They are formed by the ALE + PLE, with the PME separated. This arrangement can be found in Austrochilidae and especially in most Theridiidae and Linyphiidae, for example. Diads also occur in groups characterized by a secondary loss of the PME, such as Scytodidae.

INTERPRETATION

The assumption that eight eyes arranged in two transverse rows were already present in the ground pattern of the Araneae is not supported by any concrete fact; nor would this at all correspond with the situation in the nearest outgroups. It would mean that triads and triad-like arrangements of the lateral eyes in spiders were classifiable as parallel developments (homoplasies). This is unlikely. In accordance with the position of the eyes in the Amblypygi and Uropygi, we expect that the laterals were primarily grouped as triads (ALE + PLE + PME). This hypothesis is supported by five arguments:

a) Triads of major lateral eyes (lenses) already existed in Devonian Trigonotarbida; hence, triads apparently form part of the ground pattern of all pulmonates among arachnids.

b) The postulated configuration is in good agreement with the arrangement of the eyes in the direct outgroups.

c) Triads and semi-triads present in various groups of the Mygalomorphae and also of the Araneomorphae must no longer be explained by assumed parallel origin.

d) Various types of somewhat dissociated lateral eyes can be explained by a secondary separation of the ALE or of the PME from the others, which frequently remain in contact with each other.

e) Simon's 'oculi laterales utrinque contigui' (e.g., 1894: 517), that is to say, the occurrence of diads can be explained as part of the original triad.

To some extent, the question remains open, as to how it is possible to distinguish between eye positions that can be regarded as more or less modified triads and other positions, with secondarily approximated ALE and PLE.

PERSPECTIVES

Apparently, plagiognathy is part of the ground pattern of the Araneae. Developments in the directions of orthognathy and labidognathy can easily be explained as divergent evolutionary changes (Fig. 3). The question therefore arises of how these might be correlated with functional aspects. As an impetus for further discussion, we propose the following working hypotheses:

a) In the Mygalomorphae, orthognathy may be correlated with the capture of prey on the ground. Under such conditions, the two parallel fangs of the chelicerae can easily penetrate the victim on a substrate like two stabs of a dagger. It seems remarkable that a semi-orthognathous position of the chelicerae has originated secondarily in the Dysderidae: they kill woodlice on the substrate.[1]

b) In the Araneomorphae, the origin of labidognathy may be correlated with the evolution of capture webs (sheet, frame, orb webs etc.). These could make it more efficient to bite the prey with two opposing chelicerae or fangs, whereas plagiognathous and, even more, orthognathous chelicerae might not penetrate but rather push away the victim: there is no longer any substrate 'supporting' prey animals.

c) Plagiognathy and the maintenance of lateral triads or semi-triads of eyes apparently form part of the ground pattern of spiders; these features are confined to more 'primitive' groups. The presence and the various types of transformation of these two characters should be integrated into current concepts on the phylogeny of the Araneae (see, for example, Raven, 1985; Coddington, 1990). At present, our view of features of an araneid ground pattern and succeeding evolutionary changes seems to be somewhat at odds with various published cladograms; they hence could be partially wrong. We feel that this conflict may be due to the possibility that characters assumed to be synapomorphies in various cladograms (see,

[1] But see Kaestner (1953a: 62). He believed that the position of the chelicerae in *Dysdera* was a 'phylogenetic link' between orthognathy and labidognathy. Unfortunately, he was not aware that the first postembryonic stages were nearly labidognathous, with relatively shorter basal segments and only slightly oblique fangs (pers. observ.). In *Dysdera*, the final semi-orthognathous position was gradually acquired in later instars.

e.g., Platnick and Shadab, 1976, fig. 1; Raven, 1985, fig. 1) may well turn out to be symplesiomorphies; e.g., Raven's characters 35 (eyes spread widely across the prosoma; same as Platnick and Shadab's character 1) and 36 (male pedipalps: conductor of bulb present; see Kraus, 1978, figs 12, 14-16).

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POLYNESIAN THOMISIDAE - A MEETING OF OLD AND NEW WORLD GROUPS

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The Polynesian thomisid fauna is postulated as consisting of an Hawaiian-east Polynesian New World group, living mainly in isolated populations in the mountains and of representatives of two western lowland groups originating from Australia and Southeast Asia. The former group has apparently speciated into numerous endemic species, while the latter groups are represented by a single, widespread species and a rare Tongan species, respectively. The ranges of the eastern and western groups do not overlap. The species of New World origin have been described or previously attributed to *Misumena*, *Misumenops*, or *Synaema*. All such species are included here in *Mecaphesa* Simon, 1900 with the type species from Hawaii. *Misumenops* F.O. Pickard-Cambridge, 1900 has the type species from Eastern Brazil and has no close relatives in Polynesia or in the Old World. A widespread Old World group is also recognized here and tentatively included in *Massuria* which appear to be related to the New Guinean *Loxoporetes*. *Diaea* as currently recognized is polyphyletic and the species occurring in west Polynesia (*Diaea praetexta* (L. Koch, 1865)) is postulated to belong to a group requiring a new generic delimitation and name. *Hedana subtilis* L. Koch, 1874, also of Asian origin is here regarded as having affinity with *Tharrhalea*. The poorly described thomisid species of the isolated, southernmost island group of Polynesia, Rapa Island has not been studied. □*Araneae, Thomisidae, Polynesia, biogeography.*

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Many zoogeographical discussions, including spiders, are flawed because of poor taxonomy. The zoogeography of the Polynesian spider fauna has been discussed by Berland (1927, 1928, 1929, 1930, 1933, 1934a, b, c, 1935a, b, 1937, 1938a, b, 1942, 1947), but his discussions were based on unrevised taxa. His conclusions were often affected by misidentifications and unevenness of data available. Most spiders for these papers consisted of assorted samples made by non-specialists and many were synanthropic species found near villages.

I have been working towards a zoogeographical synthesis of the Polynesian spider fauna for ten years. Extensive personal field work in mountain tops, but also in the disturbed zone has been the most important method in the elimination of anthropochorous dispersal and distinctly synanthropic species from all speculations on the origin of the fauna of natural habitats.

The taxonomic revision of all families present seems to be necessary for any valid zoogeographical conclusions. As the first step I have carried out a 'generic' revision of Polynesian families which allows the placing of most Polynesian species groups of spiders into named or still unnamed groups of supraspecific taxa instead of zoogeographically useless concepts such as the 'worldwide' *Misumenops*, *Theridion*, *Hahnia*, or *Leucauge*. Some recent papers on Polynesian spiders have been published (e.g. Marples, 1955a, b, 1957, 1959, 1960, 1964; Berry and Beatty, 1987; Beatty and Berry, 1988; Beatty *et al.*, 1991). I have previously discussed some aspects of the spider zoogeography of the Pacific region (Lehtinen, 1980). Polynesian thomisids have also been described by Strand (1913).

The evolution of Polynesian Thomisidae has resulted in the most striking example of local speciation of spiders in Polynesia. The Thomisidae discussed comprise only the subfamily Thomisinae in the sense of Suman (1970) and various other authors. The Philodromidae are not a sister group of Thomisidae, but rather of the Heteropodidae.

The geological history of the Polynesian archipelagoes is now well known (Wilson, 1963; Duncan and McDougall, 1974; Dalrymple *et al.*, 1975). An ancient continent of Pacifica has been proposed (with differing placement and size) marginally affecting to the historical zoogeography of Polynesia (e.g. Nur and Ben-Avraham, 1977; Craw, 1983). Most geophysicists agree that the Polynesian islands are not parts of ancient land masses broken by processes of the plate tectonics, but rather chains of current islands and

seamounts representing former islands (Dalrymple *et al.*, 1975).

The origin of the Polynesian fauna therefore can be explained only by long distance dispersal from different directions (Gressitt and Yoshimoto, 1963) and partly by intrapolynesian speciation processes within the island chains (cf. also Carson, 1984; Fosberg, 1991). The use of the basic principles of the vicariance biogeography (Nelson and Platnick, 1981) will be essential for explaining the origin of groups of biota with complex patterns in their recent ranges. Craw's (1978) variant of panbiogeography, later named spanning-tree biogeography by Platnick and Nelson (1988) is a useful method for comparisons of area including also permanently oceanic island groups and it can be recommended for the analysis of many other groups of spiders. When patterns of distribution are very simple and anthropochorous dispersal in historical time has not thoroughly obscured the original patterns (cf. Stoddart, 1968), conclusions can be made with Craw's method such as have actually long been used by zoogeographers (e.g. Gressitt, 1961) before the concept of 'the most parsimonious area relationship' was defined and named.

In spite of the current taxonomic confusion of the Thomisidae on a global scale some generalisations on the zoogeography of the family are possible in the Pacific area. This paper presents the suggested relationships and zoogeography of the Thomisidae of Polynesia according to rich new material and results of my unpublished revisional work.

TAXONOMIC REMARKS

The nominate subfamily of Thomisidae should be called Thomisinae, although the name Misumeninae has been widely used, also, e.g. recently by Dippenaar-Schoeman (1983). Two groups of greenish or yellowish species without abdominal modifications are easily recognizable, one with conspicuous modifications in the ocular area (*Thomisus*-group), the other without such modifications (*Misumena*-group). The limitation of thomisine groups has been vague. Simon (1895) originally listed *Misumena*, *Heriaeus*, and *Diaea* in different tribes, while at the other extreme, the *Misumena*-group of Dippenaar-Schoeman (1983) includes not only *Thomisus*, but also *Runcinia*.

No phylogeny of thomisine groups is known and detailed discussion is beyond the scope of this study. However, the *Misumena*-group has apparently retained many plesiomorphic characters. Some groups with striking individual adaptive modifications (e.g. *Heriaeus* and *Runcinia*) may be closely related to this group.

There are most probably many other endemic species of Thomisinae in the mountains of French Polynesia, but a revision is excluded here.

The definition and delimitation of thomisine genera has been based traditionally on a few adaptive characters, including number, length, and type of setae on the carapace (Simon, 1895; Mello-Leitão, 1929; Schick, 1965; Tikader, 1980; Dondale and Redner, 1978; Levy 1985; Ono, 1988), but little attention has been paid to general patterns of the genital organs and type of sexual dimorphism. In contrast to conventions in the taxonomy of other spider groups, the naming of individual setae of the thomisid carapace has been used by some recent specialists (Schick, 1965; Dippenaar-Schoeman, 1983). This terminology is widespread in acarine taxonomy.

Some genera have been very obscurely defined and therefore all catalogues list them as being very widespread and species rich, e.g. *Misumena, Misumenops, Diaea*, and *Synaema*. All these generic names appear in thomisids described or listed from Polynesia. Even a superficial comparison of the descriptions or type material from many species of these genera (L. Koch, 1874; Kulczynski, 1911; Chrysanthus, 1964; Tikader, 1980) reveals that they are typical 'waste-basket' groups, where most species are not closely related to the respective type species.

The phylogenetic classification of the west Polynesian '*Diaea*' and the east Polynesian '*Misumenops*' has been time-consuming, as all basic taxonomic work on Indo-Pacific and Neotropical Thomisidae was done before modern taxonomic principles and methods became established. Most structural characters used as generic criteria in Thomisidae seem to be minor convergently evolved adaptations. The type species of all three large widespread genera in question, *Misumenops*, *Diaea*, and *Misumena*, are atypical or 'peripheral' species, not closely related to the Pacific species. Actually the placing of many tropical species in these three genera have been repeatedly changed, depending mainly on emphasis laid on single adaptive characters, e.g. type and pattern of setae on carapace, pattern of leg spines, eye pattern, etc.

The setation of the carapace is variable in the Polynesian groups of Thomisidae. Nevertheless, in *Mecaphesa*, sympatric species may be best identified by differences in length and density of

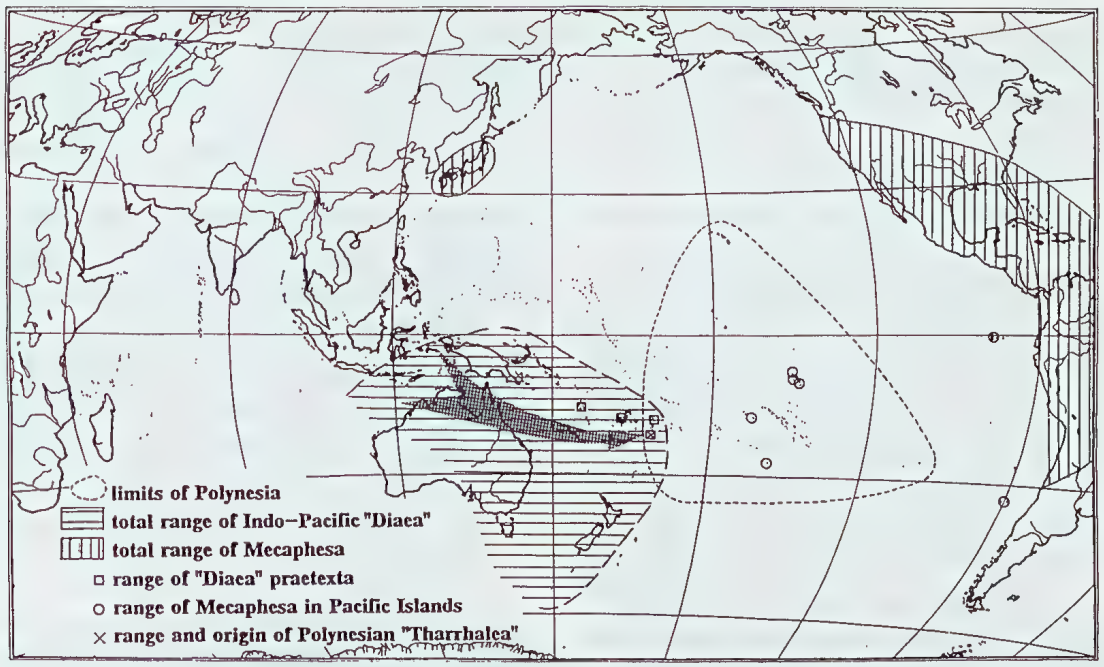
limits of Polynesia
total range of Indo–Pacific "Diaea"
total range of Mecaphesa
range of "Diaea" praetexta
range of Mecaphesa in Pacific Islands
range and origin of Polynesian "Tharrhalea"

FIG. 1. Geographic ranges and source of Polynesian thomisid groups.

the carapace setae. The shape of the carapace is variable in *Mecaphesa*, while the shape of the abdomen is variable in both '*Diaea*' and *Mecaphesa*, even within one population.

The colour pattern is variable also, although the 'usual' colouration for most species provides a reasonable guide to identification, if large populations are available.

POLYNESIAN THOMISIDS OF NEW WORLD ORIGIN

Most east Polynesian thomisids have been long included in *Misumenops* F.O. Pickard-Cambridge, 1900 (Berland, 1933, 1934b, 1942; Suman, 1970), although Roewer (1954) transferred all Hawaiian species to *Misumenoides* F.O. Pickard-Cambridge, 1900.

Many Hawaiian and North American species of *Misumenops* sensu Schick (1965) were originally described in *Misumena* or *Diaea*, and Neotropical species also in *Metadiaea* Mello-Leitão, 1929.

The adaptive radiation of Hawaiian Thomisidae indicates that essential changes in the shape of the carapace are possible without other than minor changes in the male palpal structure. The Hawaiian thomisid species were listed by Simon (1900) in *Misumena* (6 spp.), *Diaea* (2 spp.), *Synaema* (4 spp.), and *Mecaphesa* (2 spp.), but by Suman (1970) in *Misumenops* (14 spp), *Synaema* (1) and *Mecaphesa* (3 spp.). I have checked the type material of all Hawaiian thomisids preserved in the Bishop Museum and, in my opinion, both male and female genitalia of *Synaema naevigerum* Simon, 1900 are much closer to the genitalia of all Hawaiian '*Misumenops*' than those of the type of *Synaema, S. globosum* (Fabricius, 1775) from Europe. The relative width of the ocular area is certainly a parallelism in true *Synaema* and the Hawaiian '*Synaema*'. The blunt setae of *Mecaphesa* s. str. have been independently modified, and the three species constitute a sister group of the Hawaiian '*Misumenops*' and '*Synaema*' together. The genital organs of both sexes are again more or less similar and not at all related to *Oxyptila* or *Heriaeus*, as claimed by Simon (1900). Suman (1970) was not familiar with the Palaearctic thomisids and had no opinion on this matter, but be published useful drawings of the genitalia of all Hawaiian thomisids. This group of '*Misumenops*' is also present in Japan, as *Misumenops kumadai* Ono, 1985 and in western North America at least 13 species (*celer*-group), listed by Schick (1965) in *Misumenops (Misumenops). Misumenops inclusus* Banks, 1902 from Galapagos Islands and *M. sjoestedti* Berland, 1924 from Juan Fernandez Islands are

SE Asian/Australian origins (western lowlands)	Neotropical origins (eastern highlands)	Uncertain origin (Rapa)
'Diaea' praetexta belongs to probably new group *'Hedana subtilis'* belongs to *Tharrhalea*	Species previously attributed to *Misumena, Misumenops* and *Synaema*	'Misumenops' *rapaensis*

TABLE 1. Hypothesis of generic placement and zoogeographic origins of species groups of Thomisidae represented in Polynesia.

additional members of this genus in the Pacific region.

The generic name *Misumenops* is here reserved for the group of Neotropical species that are unambiguously related to *M. maculissparsa* (Keyserling, 1891), a species with a well developed tutacular process in cymbium and a complex of tibial apophyses that is widely different from any Pacific species. *M. pallens* (Keyserling, 1880) and *M. pallida* (Keyserling, 1880) were recently revised by Rinaldi (1983) without comparison to the type species. These widespread Neotropical species are not close to *M. maculissparsa*, but they may remain in the same genus. On the other hand, the concept of *Mecaphesa* is here widened to also include most Polynesian, some other Pacific and many north American *'Misumenops'*, the more plesiomorphic branch of this genus. *'Misumenops' rapaensis* Berland (Berland, 1934) from the isolated Rapa Island with a terrestrial fauna of peculiar affinities probably belongs elsewhere.

The widespread Holarctic *M. tricuspidatus* (Fabricius, 1775) is removed from this genus, but its final generic placement must wait for a more complete revision of Thomisinae: Misumenini. The structure of the male tibial apophysis, including the microstructure of its tip, is different from all other thomisids known to me. *M. japonicus* (Bösenberg and Strand, 1906) is a relative or even a member of *Diaea*, while the *asperatus* group of *Misumenops* (Schick, 1965) may belong to *Metadiaea* and the *coloradensis* group represents a distinct genus, not close to *Mecaphesa* or *Misumenops.*

The synonymic history of *Metadiaea* is confusing, too, as the authors discussing this problem (Toledo Piza, 1937; Caporiacco, 1954; Rinaldi, 1983) have based their opinions on the data from speices other than the type species, *M. fidelis* Mello- Leitão, 1929 from Minas Gerais, Brazil. I agree with Rinaldi (1983) in transferring the other species to *Misumenops pallida*-group, but not the type of the genus, and *Metadiaea* remains a valid American genus probably including also North American species.

There is a widespread Southeast Asian-New Guinean group with short scutate male abdomen and with genital organs of both sexes close to *Runcinia*. Their male tibial apophysis is similar to *Mecaphesa*, including the characteristic ribbed tip. The New Guinean *Loxoporetes* known only by the female is probably related to, or even congeneric with this group, of which most species have been described as *Misumena.* This group will probably be named *Massuria* Thorell, 1887 and it might be a plesiomorphic sister group of the widespread and widely sympatric *Runcinia.*

POLYNESIAN THOMISIDS OF OLD WORLD OR AUSTRALIAN ORIGIN

The greenish thomisids from Samoa and Tonga islands have been described as different species (L. Koch, 1874; Rainbow, 1902: New Hebrides; Strand, 1913), all referred to *Diaea.* A critical survey of several large populations reveals that there is only one widespread species, *'D.' praetexta* (L. Koch, 1865) with large infrapopulational variation in the colour pattern, but quite small variation in the structure of the genital organs. In contrast to east Polynesian and Hawaiian thomisids this species lives in the vegetation of lowlands and is also common in Fiji and Vanuatu.

At least *D. sticta* and *D. limbata* (Kulczynski, 1911) within the widespread and common Melanesian *Diaea* spp. as well as the east Australian *D. multopunctata* L. Koch, 1874 and *D. prasina* L. Koch, 1876 are congeneric with *D. praetexta.* This group of Australian-Polynesian *'Diaea'* deserves generic status, but until some 'old' thomisine genera from the Indo-Pacific area have been revised the erection of a new genus would be hasty. The type species of *Diaea, Araneus dorsatus* Fabricius, 1775, probably together with some other Palaearctic species has male and female genital organs resembling *Heriaeus* (Loerbroks, 1983). The deviating non-genitalic characters of *Heriaeus* are adaptations to life in the desert.

Hedana subtilis L. Koch, 1874 was described from one male and a juvenile from Tonga, western Polynesia. Most probably it is not congeneric with the Australian type species *H. gracilis* L. Koch, 1874 and several other species

from Southeast Asia to New Zealand. It has not been compared with the type of *Tharrhalea* from N. Australia, but it seems, at least, to belong to the same tribe as *T. maculata* from New Guinea. *H. pallida* Koch, 1876, described from juvenile specimens from Tonga most probably is a synonym of *H. subtilis* or even '*D.*' *praetexta*. In addition to these two very old records there is also a recent record of a subadult female from Tonga. *Hedana* and *Tharrhalea* have been catalogued in Stephanopinae (Simon, 1895; Roewer, 1954; Bonnet, 1957), but '*H.*' *subtilis* belongs to Thomisinae.

I have seen relatives of *H. subtilis* (? *Tharrhalea*) in New Guinea and southeast Asia and the range of this unnamed group is more or less similar, but possibly extending farther northwards, when compared to that of the '*Diaea*' *praetexta*-group.

ZOOGEOGRAPHICAL CONCLUSIONS

The Polynesian thomisid fauna has apparently arrived from two opposite directions, South America and Melanesia. These two elements are not known to be mixed in any part of Polynesia (map in Fig. 1).

New World element (*Mecaphesa*) probably first arrived in Hawaii, where an explosive speciation has taken place, resulting in 17 known species (Suman, 1970: in three genera), most having a small range up in the mountains. Galapagos Islands (1 or several spp.) and Juan Fernandez Islands constitute another possible source of immigration for the East Polynesian *Mecaphesa* spp. They have further evolved to at least six, but probably more local endemics. There are also sympatric montane species, at least in the Marquesas Islands, but most probably also in Tahiti. The majority of East Polynesian species live on mountain tops, but a few species have occassionally been recorded also in lowland.

The Oriental-New Guinean genus of the *Misumena*-group, here tentatively called *Massuria* has not been found in the intervening Melanesian archipelagoes and must be excluded from possible sources of origin of the east Polynesian *Mecaphesa*, although both groups belong to Misumenini, a group probably older than any mid-Pacific archipelagoes.

There are no known thomisids in the Central Polynesian islands (Cook Islands, Tokelau Islands, Niue, etc.) (Marples, 1955b, 1957, 1960, 1964) or in the low coral islands north of Samoa (Rainbow, 1897; Roewer, 1944). In spite of additional collecting both in the lowland as well as in the mountains of Rarotonga by myself, no *Mecaphesa* spp. have been observed. The absence of *Diaea praetexta* in disturbed lowland habitats of Rarotonga seems to show that anthropochorous dispersal of this species is not very effective, although its frequency in the more western archipelagoes can be partly explained by this type of short distance dispersal.

The Australian Thomisidae appear to have arrived through Melanesia, where Fiji and Vanuatu share the same common lowland species, '*Diaea*' *praetexta* and several closely related species are present in New Guinea and Eastern Australia. The other west Polynesian thomisid species, '*Tharrhalea*' *subtilis* belongs to a group that has a wider range including southeast Asia. In spite of intensive field work in Samoa and Tonga during 1991-92, there are still no montane thomisids known in the western archipelagoes of Polynesia.

There are some other Polynesian spiders of Neotropical origin (Anyphaenidae, some Theridiidae, etc.), but most spider families represented in Polynesia are of Melanesian, southeast Asian or New Zealand origin.

ACKNOWLEDGEMENTS

This study is part of a long range programme on Indo-Pacific spiders, including field and museum work during the last 20 years. This work has only been possible through the generous cooperation of numerous persons, who could not be listed separately here. Useful comments were also presented by two referees and an editor. The map was kindly drawn by Ms. Maija Mustonen, and the original English text was checked by Mrs Alice Moore.

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SCORPION DISTRIBUTION IN A DUNE AND SWALE MALLEE ENVIRONMENT

N.A. LOCKET

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A system of stable and vegetated dunes, separated by occasionally flooded swales, contains populations of six scorpion taxa. *Urodacus yaschenkoi* (Birula) digs deep burrows in the soft soil of the dunes, but the shallower burrows of *U. armatus* Pocock are concentrated at their base, extending onto the swale for ca. 50m. *Lychas jonesae* Glauert, *L. variatus* (Thorell) and *Isometroides angusticaudis* Keyserling occur on the swale but not the dunes. *Cercophonius kershawi* Glauert has occasionally been found in litter beneath mallee trees on the dunes. Soil hardness may account for *U. yaschenkoi* occurring only on the dunes. *Isometroides*, a spider predator, occurs where spider burrows are found. Predation by the larger *Urodacus* may account for the buthids not extending onto the dunes.□ *Scorpions, Australia, ecology, habitat.*

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An area of scrub near Berri in the South Australian Riverland consists of a series of stable dunes bearing mallee trees and shrubs interspersed with flat grassy swales, which show signs of occasional flooding. This locality contains a population of *Urodacus yaschenkoi*. Blacklighting on and between the dunes showed that five other scorpion taxa are present in the area but not uniformly distributed. Observations are now presented on these populations and their distribution across the dune- swale system.

Two of the taxa found do not accord with the descriptions given by Koch (1977). One, a *Lychas*, corresponds to Glauert's (1925) unillustrated description of *L. jonesae*, apparently from a single specimen collected near Kalgoorlie, Western Australia. Koch (1977), who examined the holotype, included *L. jonesae* in *L. marmoreus* but did not give reasons for doing so. The present specimens resemble *L. alexandrinus*, widely distributed in arid Australia (Koch, 1977, map 4), but differ significantly from it and from *L. marmoreus*. They agree closely, except in colouration, with the (markedly faded) type of *L. jonesae*. An illustrated redescription of *L. jonesae* is in preparation, and the present specimens referred to that species meanwhile.

The other belongs to the genus *Isometroides*, which Main (1956) suggested was monospecific, all specimens being referable to *I. vescus*, a view supported by Koch (1977). The Berri specimens agree better with the descriptions of Keyserling (1885), Kraepelin (1916) and Glauert (1925, 1963) of *I. angusticaudis*, and are certainly not typical of *I. vescus*. An account of the genus *Isometroides* is in preparation, and the present specimens referred to *I. angusticaudis* in anticipation of that work.

Many factors influence the distribution of scorpions, including latitude and climate, type of terrain and soil hardness. Biotic factors such as intra-guild competition and predation are also important (Polis, 1990). The latitude of the study site, ca 34°, is within the range of maximum scorpion diversity, given by Polis (1990) as 23-38°. Within this belt up to ca 10 species may occur sympatrically in the northern hemisphere, though most locales have only 3-7. Diversity is greatest in desert regions, with 24 of the 28 communities of six or more being in subtropical deserts, where terrain may range from loose sand to hard packed stony ground. Soil hardness was closely related to species distribution in *Opisthophthalmus* by Lamoral (1978). Bradley (1986) showed that populations of the burrowing *Paruroctonus utahensis* were denser on soft soils than hard, and that its burrowing was impaired by the hardening of the soil due to rain. Vegetation patterns correlated both with soil type and scorpion population, but areas with different scorpion densities contained similar biomass of potential prey. Bradley also demonstrated the destruction caused by flooding to a population of *P. utahensis*.

Polis (1990) shows that biotic factors may well affect the composition and balance of a population. He gives strong evidence on the important influence of scorpions on the community in which they live, by competition through predation on other invertebrates or cannibalism of smaller scorpion species, and of smaller conspecific instars. Individual scorpions of different species but similar size may well compete direct-

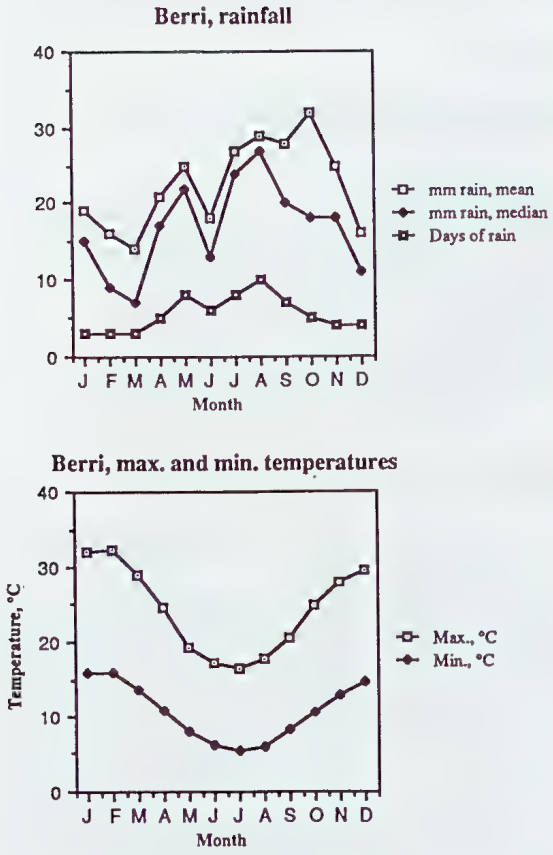

FIG. 1. Temperature and rainfall, Berri (nine year average).

ly for food, since most are generalist predators, perhaps leading to one species becoming dominant. Different sized scorpions may take different groups of prey, based on size, though the young of a large species may compete directly with adults of a smaller when the individuals are of comparable size.

METHODS

The site is about 8 km NNE. of Berri, 140°38'E, 34°13'S, in the South Australian Riverland. The climate at Berri is warm and dry (Fig. 1). A transect 10m wide was laid out from dune to dune across a swale, some 300m. The nature of the soil was noted, and trees and shrubs more than a few cm high plotted to the nearest 1m.

Single-, or on one occasion two-day, visits were made to the study site on fourteen occasions, on moonless nights when possible, between March 1989 and May 1992. On each visit the

Date	*U.yasch.*	*U.armat.*	*I.angust.*	I.variatus	*L.jonesae*
16 Sep 89	0	0	4	0	0
24 Mar 90	4	3	4	0	1
15 Sep 90	0	1	2	0	3
20 Oct 90	0	0	10	0	7
10 Nov 90	0	0	6	0	27
15 Dec 90	0	0	11	2	21
15 Jan 91	0	0	11	0	16
16 Mar 91	0	11	0	0	18
5 Oct 91	14	14	2	2	1
2 Nov 91	0	0	5	0	1
7-8 Dec 91	9	6	5	1	70
2 Feb 92	1	1	1	0	41
29 Feb 92	6	11	11	1	59
2 May 92	0	2	6	1	
TOTAL	34	52	78	6	265

TABLE 1. Catches of scorpions, blacklighting only.

parts of the transect containing the characteristic burrows of *Urodacus yaschenkoi* were noted. On one occasion in summer all the burrows within the transect were marked with numbered tags. Burrow identification was confirmed and specimens obtained by trapping burrows away from the transect. The traps were plastic vending machine cups, ca 200cc capacity, dug into place at the burrow mouth, the burrow opening directly at the lip of the cup. The traps were visited at least 1h after sunset, when scorpions had emerged from the burrows and fallen into the cup.

Smaller burrows, without the curved entrance of *U. yaschenkoi*, were identified as those of *U. armatus* by digging out the scorpion. On three occasions *U. armatus* was identified by blacklight at a burrow mouth which was then marked and examined next day.

Blacklighting was carried out, away from the transect but within the dune-swale system, on each visit by two persons, working parallel to each other and approximately 100m apart. Blacklighting, commencing at various times after sunset, on some occasions as soon as it became dark enough and on others up to 1.5h after sunset, was continued for ca 2h.

Urodacus yaschenkoi and *U. armatus* could be distinguished in the field by blacklight. *Isometroides*, except very small individuals, was distinguishable from the *Lychas* species, but the two *Lychas* could not be told apart until the catch was examined indoors. This took place on return from the field, when notes on weather, capture sites and behaviour were written. Detailed plots of specimen location were not made, but it was possible to assign the taxa to dune, dune base or

FIG. 2. View of transect across swale, looking north from southern dune. 1, sandy soil at base of dune. 2, low bank beside old track. 3, track. 4, swale. 5, far dune. See also Figs 3 and 4.

swale. Identifications were confirmed on return to the laboratory.

RESULTS

The transect, running N-S, extends 300m from the top of one dune, ca 6m high, across the flat swale, to the top of the next dune (Fig. 2). The dunes bear scattered mallee trees, *Eucalyptus oleosa* and *E. brachycalyx*, numerous bushes of native hop, *Dodonaea* sp., and clumps of *Spinifex*. The swales are lightly covered with grass and other low plants, with sparse bushes of native hop and of *Cassia nemophila* var. *platypoda* (Fig. 3).

Catch data are summarised in Table 1 and distributions in Fig. 4. *Urodacus yaschenkoi* burrows occur on the dunes, mainly in the open but a few under light cover. In January 1991, 80 burrows were located and marked within the transect, but by October, 56 tags either were not related to a visible burrow or had been disturbed by animals. Of the three *U. armatus* burrows marked while blacklighting, two had been closed by next day, and would have been missed apart from the marker. No further attempts were made to trace the fate of individual burrows. Individual *U. yaschenkoi*, usually adult males, were found by blacklighting in December-February, mainly on the dunes but including one ca. 50m onto the swale. *U. yaschenkoi* were also observed at their burrow mouths by blacklight in summer.

Urodacus armatus burrows were occasionally found on the dunes, but most were at the dune base and for up to 50m onto the swale. *U. armatus*, mostly immature, found by blacklight had a similar distribution , with occasional examples up to ca 100m onto the swale. Immature individuals have sometimes been found clinging to low vegetation within a few cm of the ground. *U. armatus*, recognisable by blacklight from *U. yaschenkoi* by their squat pedipalps, have been seen at the burrow mouth between October and February.

Three species of buthid, *Lychas jonesae*, *L. variatus* and *Isometroides angusticaudis* have been found, only on the swale, by blacklighting. *L. jonesae*, commonest overall, though on occasions outnumbered by *I. angusticaudis*, occurs all across the swale, but often near low vegetation near the dune base. Some have been found clinging to stems within a few cm of the ground,

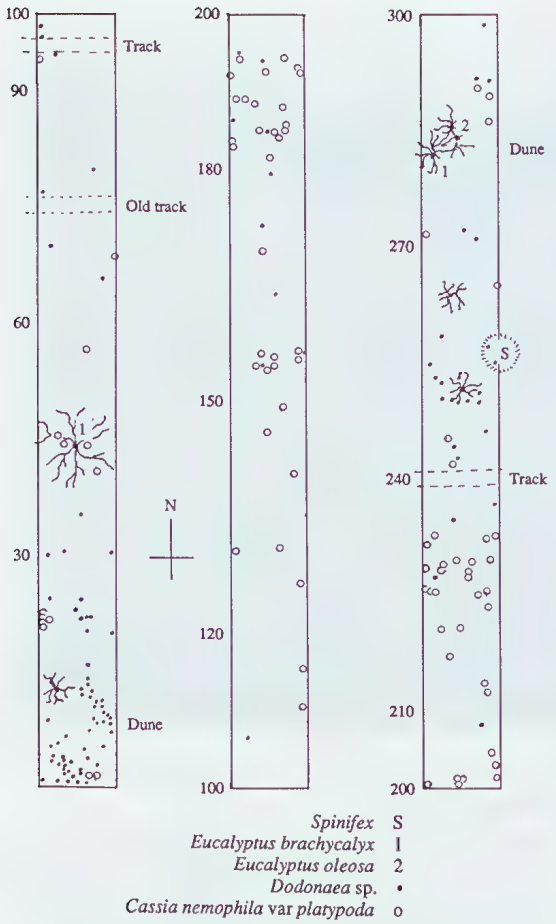

FIG. 3. Plot, to scale, of distribution of major plants across transect. Distances in metres.

mostly head down, but none have been found high in bushes.

Lychas variatus has been taken occasionally, never more than two and frequently none, in an evening. Insufficient have been found to comment on their distribution on the swale.

Isometroides angusticaudis has mostly been found on the surface by blacklight, among low grass rather than taller vegetation and extending up to but not above the dune base. A few have been dug by day from the burrows of lycosid spiders, abundant on the swale but not the dunes.

One *Cercophonius kershawi* (identified from Acosta (1990)) was found in May 1992 by kicking over leaf litter beneath mallee trees while blacklighting. (Two juvenile *Lychas variatus* were caught in the same way on dunes within 1 km of the transect in June 1987).

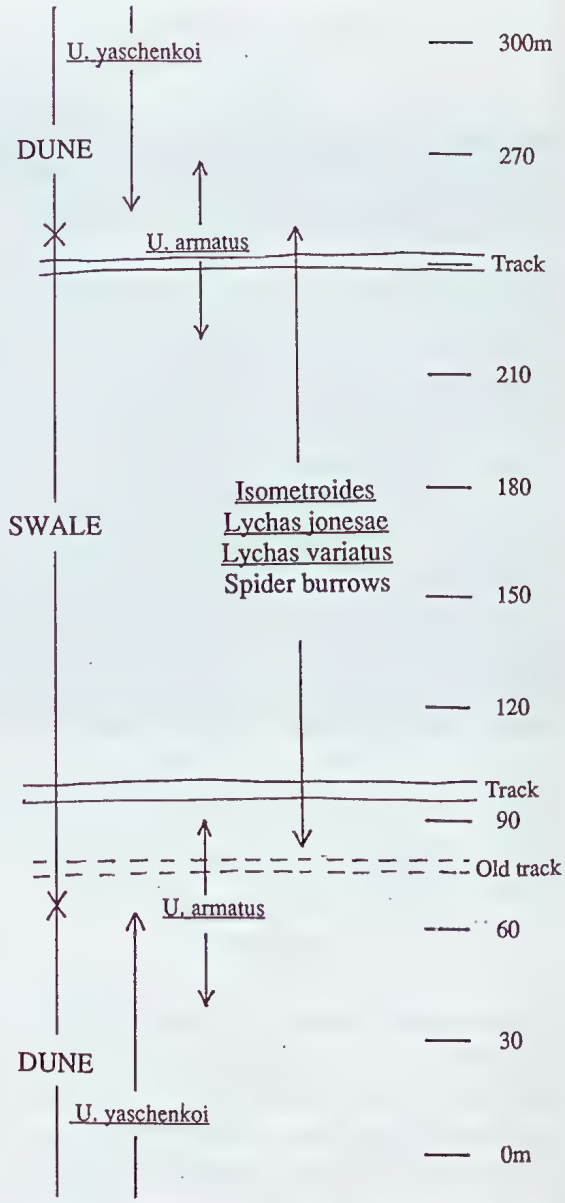

FIG. 4. Distribution of scorpions across dune and swale system. *Urodacus yaschenkoi* occurs on the dunes, *U. armatus* at their bases and the three buthids on the swale.

DISCUSSION

Many labels in collections state a locality, without details of microhabitat. The population disparity now described from localities a few meters apart suggests that it may be helpful to define localities more precisely.

Lamoral (1978), studying two burrowing

species of *Opisthophthalmus*, found clear separation of two otherwise sympatric species, strongly correlated with soil hardness, a factor probably also important in *Urodacus*. Koch (1978) found the depth and tortuosity of *Urodacus* burrows within a species greater with aridity. There is also a species difference: *U. yaschenkoi* and *U. hoplurus* dig deeper and more spiral burrows than *U. armatus*. Koch (1981) noted that *Urodacus* scorpions show little correlation with soil type, but more with softness and the chance of reaching water by burrowing. Shorthouse (1971), Shorthouse and Marples (1980) and Koch (1978) have described the spiral burrows up to 1m deep of *U. yaschenkoi* in loose sandy soil. The dune soil at Berri is of this type. Most burrows of *U. armatus*, seldom more than 30cm deep, are in the firmer soil at the dune base and swale, though some occur up the dunes, in what appears otherwise to be *U. yaschenkoi* territory.

Koch (1981) considered three Australian zones, a moist temperate southern, semi-arid to desert central and humid tropical northern, associating various scorpions with these zones: *Urodacus yaschenkoi* and *U. armatus* he regarded as mainly central forms. He found scorpion distribution not correlated with vegetation type, single species occurring in a wide range of habitats. He suggested that range-determining factors include temperature, precipitation and biotic factors, e.g. competitive exclusion. He also examined morphological characters, suggesting that large size, longer metasomal segments and spines, more granulation, and higher pectine tooth counts are aridity-linked in *Urodacus*, while large size, light colouration, more granulation, higher pectine tooth counts and a less prominent subaculear tooth are aridity- linked traits associated in *Lychas*. He regarded *Isometroides* as showing the culmination of these buthid traits. Of the sympatric species at Berri, both *Urodacus* are pale and smooth, their pectine counts largely overlap, but *U. yaschenkoi* is large and *U. armatus* small. *L. variatus* and *I. angusticaudis* are both pale but mottled though *L. jonesae* is small and dark, with subaculear tooth intermediate between the other two buthids.

The swale, where *Isometroides* has been collected by blacklight, contains numerous lycosid spider burrows, up to 30cm deep in hard soil. *Isometroides* was recognised by Main (1956) as a spider predator and collected by her from their burrows. Four have been so collected in the present study, but no concerted digging has been done.

The habit of clinging to vegetation close to the ground, also observed in immature *U. armatus* by G.T. Smith (personal communication), may enable scorpions to avoid wandering predators. Some scorpions, e.g. *Centruroides exilicauda* in America, are frequently found in bushes well off the ground, but such climbing has not been seen in the present case.

The total catches of buthids suggest that *Lychas jonesae* is dominant on the swale, though on occasions more *Isometroides* have been caught. *L. variatus* is much less common than either. *Isometroides* is known to be a specialist burrowing spider predator. Probably the *Lychas* species are less specialised, though little is known of their diet; one instance of *L. jonesae* eating an immature *U. armatus* was the only act of predation observed. Insufficient is known of the habits of the two *Lychas* to indicate why the smaller should be commoner.

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FROM FLOOD AVOIDANCE TO FORAGING: ADAPTIVE SHIFTS IN TRAPDOOR SPIDER BEHAVIOUR

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Fossorial habits protect many mygalomorph spiders from both biotic and environmental factors. However burrows in some habitats are vulnerable to sheet flooding. Spiders in diverse habitats counter the hazard of flooding in various ways. A comparative account of adaptive specialisations, particularly of burrows, in flood avoidance is presented. Such primary modifications sometimes lead to new foraging opportunities. Examples are given of modified foraging as a consequence of burrow adaptations. The origins of such constructions are hypothesised in relation to changing climatic regimes and modified habitats. The idiopid genera *Homogona* Rainbow and *Neohomogona* Main are restored from synonymy.
□*Mygalomorphae, Trapdoor spiders, burrows, flood avoidance, foraging, Australia.*

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Most mygalomorph spiders are terrestrial and either make burrows, silk tubes or webs or combine a web with a burrow. A few are arboreal and either make tubes in the bark of trees or have webs in crevices or under bark; their nests are generally not associated with foliage. Of the 15 currently recognised families of Mygalomorphae (Raven, 1985), 10 occur in Australia and of these, seven have at least some representatives with trapdoors. A burrow provides protection from the physical environment, from weather conditions and from predators and parasites; it provides a brood chamber for eggs and spiderlings. A burrow is also a lair from which a spider perceives and ambushes or intercepts prey; thus it provides a foraging base. All these functions have been commented on many times in the literature over the last century, the earliest comprehensive study possibly being that of Moggridge (1873, 1874).

In its simplest form a burrow has an 'open' entrance from which a spider makes short sorties in pursuit of prey. In extreme habitats, the entrance may be sealed with silk or soil for added protection during certain times of the year, for example during summer drought or winter snow falls. Folding collars and finally hinged doors give maximum security and protection. The protective advantage of a door has been shown to be offset by the hinge-line inhibiting the foraging area of a spider but nevertheless many door builders have overcome this disadvantage by various modifications to the burrow (Coyle, 1981; Main, 1986).

This paper discusses the adaptive behavioural responses associated with nest structure and site, of Australian mygalomorph spiders, to the hazard of flooding and shows that these primary adaptations have sometimes secondarily created new foraging opportunities for spiders. In particular the previously unreported nest of an undescribed species of *Aname* which exhibits both 'primary' and 'secondary' responses in its flood-avoidance tactics is described also.

FLOOD AVOIDANCE BEHAVIOUR

In certain terrestrial habitats, burrows and silk tubes and webs face the physical hazard of flooding. Generally the complexity of habitats in rainforest and mesophyll forest provides some sort of buffer against flooding; there is greater capacity for absorption of rainfall in the vegetation and litter of a forest floor than there is for example in desert or semi-arid country where sheet flooding on bare ground is a common phenomenon. Even so some rainforest situations are subject to water logging and flooding associated with torrential downpours. Likewise where rain is markedly seasonal as in monsoon rainforests the alternation of wet and dry conditions means that some habitats experience sudden saturation or inundation. Main (1976, 1982b) and Cloudsley-Thompson (1982, 1983) discussed some of the burrow modifications of mygalomorphs which prevent flooding. Avoidance of flooding is different to behaviours whereby spiders withstand immersion by enclosing the body in a bubble of air.

In summary, in avoiding flooding of nest sites, mygalomorph spiders have adapted behaviourally in several ways:

(1) By moving the nest site–behaviour prior to, during or after the event.

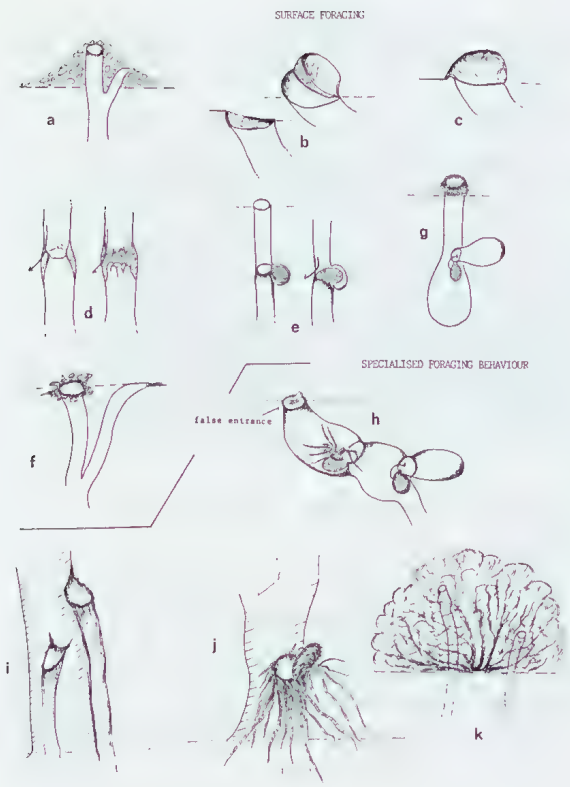

FIG. 1. Flood avoidance specialisations of mygalomorph burrows: (a) soil and pebble levee of *Kwonkan wonganensis*; (b) bath plug door (Idiopidae); (c) dome or 'cap' of an *Aganippe* species (Idiopidae); (d) 'sock' of *Anidiops* (Idiopidae); (e) 'pebble' and collar closure of burrow of *Stanwellia nebulosa* (Nemesiidae); (f) side shaft and escape 'hatch' of burrow of *Aname diversicolor* (Nemesiidae); (g) side shaft with door in nest of *Idiommata* sp. (Barychelidae); (h) profile of nest of a *Teyl* sp. (Nemesiidae) with entrance atrium and subterranean doors (and sideshaft); (i) aerial tube of *Misgolas robertsi* (Idiopidae) supported on tree trunk; (j) extended tube with trapdoor of *Aganippe castellum* (Idiopidae) supported against stem of shrub; (k) silk and soil tube of 'turret-building' *Aname* sp. (Nemesiidae) in foliage of shrub.

(2) By permanently reinforcing the nest e.g. burrow (and/or opening) against inundation–prevention.

(3) By modifying the nest structure so that part of it is safeguarded against inundation–prevention.

(4) By modifying the nest so that it is (in part) sited beyond the reach of intermittent flooding–prevention.

(5) By adopting an arboreal instead of terrestrial habitat.

Examples of these adaptations will now be given.

(1) Mygalomorphs elsewhere have been recorded as moving nest sites prior to inundation. The Amazonian web-weaving diplurid *Ischnothele guianensis* makes webs on tree trunks in the rainforest which is seasonally inundated. Spiders move their web sites higher up the trunks as the water level rises (Hofer, 1991). The Australian diplurid genus *Cethegus* (curtain web spiders), which makes copious webs sometimes associated with a burrow retreat, amongst stones, or against logs or shrub stems, is widespread across tropical Australia, the interior and southwestern Western Australia (Main, 1960, 1991a and unpublished; Raven, 1984). A study on a species at Durokoppin in the Western Australian wheatbelt showed that the spiders move their web sites after rain damage (Main, unpublished). Another species which occurs amongst the rocks of water courses in the Kimberley rainforest patches (Main, 1991a) presumably moves web sites during the 'wet' when the habitat is inundated. Although dependent on a web for prey capture these spiders are remarkably agile on the ground, and thus could readily decamp if flooded out of their nest sites, following which a web could be readily reconstructed (unlike some architecturally complex burrows of other mygalomorph families).

(2) Even 'open' burrows, if lined with silk frequently have collapsible or folding collars which can prevent flooding, for example as in many nemesiids and some *Misgolas* species, e.g. *M. pulchellus* (Rainbow & Pulleine) (pers. obs.). Collars are sometimes strengthened with litter or by a surrounding pile of soil or silk-bound pebbles (Fig. 1a) e.g. the levees of some nemesiids including *Kwonkan wonganensis* (Main) (originally described as *Dekana* (Main, 1977, plate 15)) (see also Main (1981, plate 1, fig. d) with reference to the levee of a 'diplurine' burrow). The ctenizid *Conothele*, the actinopodid *Missulena* and some barychelids have secure doors and parchment or canvas-like, silk linings which are more-or-less impermeable. Most idiopid species construct well defined burrows and all except some species of *Homogona*[1], *Neohomogona*[1] and *Misgolas* have a trapdoor. Many idiopid species which have adapted to flood-prone habitats, ranging from rainforest to desert

[1]The idiopid genera *Homogona* Rainbow and *Neohomogona* Main were synonymised with *Cataxia* Rainbow by Raven (1985). They are here formally restored from synonymy and diagnosed in Main (1985).

and particularly in bare ground or sloping creek banks, frequently have permanently reinforced burrows including thick plaster walls coated with dense silk, and thick, close fitting bath-plug like doors or tightly fitting caps (Figs 1b, c). Such secure nests also provide protection against predators, parasites and adverse physical conditions, including dessication.

(3) Some species of Idiopidae, Nemesiidae, Barychelidae and Hexathelidae safeguard particular areas of their burrows against inundation. Such safeguards include (a) special blocks in the lumen or (b) sideshafts with 'escape' hatches or (c) one or more sidechambers with 'internal' trapdoors. Examples of the above are:

(a) Some species which have either an open entrance (e.g., *Misgolas* spp.) or a flimsy door (e.g., *Anidiops*) have a collapsible collar ('sock', see Main, 1957, 1976, plate 9 and 1985, figs 209, 210) consisting of a detachable section of the silk lining which can be pulled downwards by the spider thus blocking the burrow (Fig. 1d). Water seeping down the walls or flowing into the burrow is deflected by the infolded 'neck' of the sock and soaks into the surrounding soil leaving the lower section of the silk lined burrow unflooded. A similar structure in *Stanwellia nebulosa* (Rainbow & Pulleine) (Fig. 1e) is further reinforced by an attached, artificial pebble which seals the lower silk lined part of the burrow (Rainbow & Pulleine, 1918, pl. 20; Main, 1964, 1972 figs 22a, b, 1976). Although these devices are generally considered a protection against predators (see Main, 1956a regarding *Anidiops* (=*Gaius*) their original function was probably prevention against flooding (see Main, 1976 regarding *Stanwellia*).

(b) Nests of some species have silk sideshafts with 'escape' hatches at the surface (see Fig. 1f) which probably enable the spiders to escape flooding as well as intrusive predators. Examples are the burrows of 'wishbone' spiders of the genus *Aname* (Main, 1982a, fig. 1; 1976, pl. 10) and *Misgolas ornata* (Rainbow) (Main, 1985: 33).

(c) Sideshafts with 'internal' trapdoors are constructed by several undescribed species of *Teyl* (Nemesiidae) (earlier attributed to *Ixamatus*, see Main (1976, pp. 86-88, fig. 21)), by *Hadronyche* (Hexathelidae) (see Main, 1964:40, fig. j; 1976, fig. 18c; Gray, 1984, fig. 31 (described as *Atrax*)), *Idiommata* (Barychelidae) (Main, 1976, fig. 19d; Raven & Churchill, 1991: 35) and *Missulena* (Actinopodidae) (Main, 1956b). While the sideshafts of all species studied are known to function as brood chambers and also sometimes as protection from predators it is probable that the original function was that they offset flooding of the main shaft of the burrow (see Fig. 1g). Considering the habitat of *Teyl* species this is unequivocal.

(4) Burrows of some species are continued as tubes above the ground or litter surface and may be strengthened into free standing palisades (by the attachment of leaves, twigs and debris) which deflect sheet flooding in bare ground or prevent immersion in water-soaked litter. Examples include the tubes of *Homogona cunicularius* Main (Main, 1983, fig. 15), *Misgolas hirsutus* (Rainbow & Pulleine) (pers. obs.) and *Neohomogona stirlingi* and *N. bolganupensis* Main (Main, 1985, fig. 219). Tubes that extend a considerable distance above the substrate are attached to rocks, tree buttresses, exposed roots e.g. *Misgolas robertsi* (Main and Mascord) and related species (Main and Mascord, 1974, pl. 1a, b; Mascord, 1970 pl. 2 fig. 4), logs e.g. *Cataxia maculata* Rainbow (Main, 1969, figs 30, 31) or stems of shrubs e.g. *Aganippe castellum* Main (Main, 1986, figs 2, 4i; 1987, fig. 6). The first examples have open tubes, sometimes with flanged, collapsible collars but *A. castellum* has a trapdoor (Figs 1i, j). All are effective in flood avoidance by having the entrance above the 'flood level' following a deluge.

The previously undescribed but remarkable burrow/tube of an undescribed species of *Aname* extends as a turret-like tube amongst supporting foliage of shrubs. The genus *Aname* which is widespread but endemic in Australia and Tasmania, occurs in varied habitats, is taxonomically diverse and includes many undescribed species.

The turret-building species occurs in semi-arid country in southeastern Western Australia and Eyre Peninsula in South Australia. Nests have been observed in mallee/spinifex associations (*Eucalyptus/Triodia*) (Figs 2a, b, c) but also in mulga and amongst chenopod shrubs in seasonally swampy habitats. The spiders make shallow burrows lined with silk which extend as tubes into the foliage of supporting tussocks or shrubs and open either within the foliage or above the canopy (Fig. 1k). The outside of the tube is heavily but irregularly coated with soil. During and after rain, sheet flooding occurs in such sites, and particularly in the sandy loam of mallee/spinifex associations, water flows in a slurry around the spinifex hummocks. Burrows appear to be deepened (and/or remade) after rain and the sodden spoil dumped on the lip of the tube and outside the

Siting of burrow opening		PRIMARY ADAPTATION		SECONDARY ADAPTATION
		Flood avoidance through modified burrow structures	Unmodified foraging	Specialised foraging in response to 'new' opportunities
FOSSORIAL	Ground	—open* burrows: collars& folding collars & levees	surface	
		—closed* burrows: reinforced walls & doors	surface	
	Subterranean	— sub-surcae closures of lumen (open or closed burrow)	surface	
		—supernumerary chambers with doors		subsurface (pitfall captures)
	Elevated	extension of open tubes against vertical support		arboreal and semi-aerial
		—extension of closed burrow (with door) against plant stem		arboreal
		extension of open tube into foliage		foliage canopy
CORTICOLOUS		— open or closed tubes in bark		arboreal

TABLE 1. Siting of mygalomorph burrows primarily modified in flood avoidance and those secondarily resulting in specialised foraging methods. * open = without door; closed = with trapdoor.

entrance. Thus the turret is heightened progressively while much of the paste-like spoil pours down the outside wall, solidifying into a kind of stucco as it does so. Tubes up to 25cm have been observed within the supporting scaffolding of spinifex hummocks. The sometimes bulky structures belie the relatively small size of the artificers (up to 4.5mm carapace length). Occasionally free-standing tubes (but small and only up to 10cm high), away from shrubs, are found (see Main, 1982b, fig. 2). Most unsupported tubes may collapse (at ground level) and be destroyed during flooding while at least the aerial section of those amongst the tussocks remain relatively intact.

(5) Mygalomorphs which have their nests sited completely on the trunks of trees are found only in very wet forests. Their nests in such situations appear well protected against inundation. Australian examples include theraphosids which make silk retreats under bark in north Queensland (pers. observation), the nemesiid, *Chenistonia villosa* Rainbow and Pulleine which makes defined silk tubes in crevices of *Casuarina* bark in the karri forest of southwest Western Australia (pers. observation), species of the ctenizid, *Conothele*, in tropical Queensland (Main, 1976) illustrated in McKeown (1963), the barychelid *Sason* in north Queensland (Raven, 1986) and migids e.g. *Moggridgea tingle* Main (Main, 1991b). *C. villosa* and *M. tingle* both make nests in the ground also, in sites not vulnerable to water logging. This is probably a secondary habitat adopted in response to gradual drying of the climate and environment where the bark of trees would be subject to dessication.

NEW FORAGING OPPORTUNITIES

Foraging 'techniques' of mygalomorphs are closely associated with burrow structure. Burrows of some species are constructed with special adjuncts that enhance foraging, such as silk trip threads or attached twiglines. Main (1957, 1982b, 1987) described some combinations of burrow structure, morphology and foraging behaviour in relation to the habitats occupied and noted the relative efficiency of the various foraging strategies.

In modifying behaviour and burrow structure in flood avoidance, some species have as a consequence been exposed to 'new' foraging opportunities. Table 1 summarises the categories of 'primary' burrow modifications and sitings associated with flood avoidance and any 'secondary' changes of foraging behaviour. Reinforcement to burrows and doors which do not involve alteration of siting of the entrance, do not generally result in modification of foraging method. However, any modifications which alter the siting of burrow entrances away from the surface of the ground do result in specialised (predatory) foraging behaviour.

A striking example of a subterranean entrance is that constructed by a group of *Teyl* species. Although most species of *Teyl* have open burrows, a few build doors in flood avoidance. Several species have surface doors in bare open ground but the foraging method is similar to that of species with open holes (Main, 1986). Several species which occur in deep litter in seasonally flood-prone, braided creeks and the flats around salt lakes in southern Western Australia have evolved a further specialisation. An open 'false entrance' leads into a cup-like pouch or atrium which has on its inner wall a trapdoor (entrance

FIG. 2. *Aname* sp. Habitat and turrets (a) mallee/spinifex shrubland on sandy loam soil west of Balladonia, Western Australia; (b) spinifex shrubs with 'turrets'; (c) turret in spinifex, note open entrance.

proper) which leads into the main shaft of the burrow; a second trapdoor leads from the main shaft into a blind sideshaft (Fig. 1h). These doors provide a double safety valve in the event of flooding (Main, 1976). The false entrance/atrium functions like a pit-fall trap which 'catches'

crawling insects that are then seized by the spider as it straddles the open door inside (Fig. 1h) (Main, 1982b fig. 7d). The pit-trap also provides a clear foraging area for the subterranean entrance-proper, unencumbered by the litter which would otherwise impede the plug-like door. Notable examples of elevated nests (supported against tree trunks), the primary adaptation of which has been flood avoidance but which has secondarily resulted in arboreal foraging, are those of *Misgolas robertsi* (see Mascord, 1970 p.12; Main 1976, plate B5) and *Aganippe castellum* (Main, 1986, 1987 p. 34 and fig. 6).

Spiders, the nests of which are sited on the trunks of trees but which have no contact with the ground and are thus corticolous, similarly have adopted an arboreal foraging behaviour. *Conothele* (possibly *Conothele arboricola* Pocock), *Sason* and *Chenistonia villosa* and *Moggridgea tingle* are thus all arboreal foragers although the latter two are recognised as being facultative in their behaviour. Even *Idioctis* species which extend their tubes above the tide level (or are sealed against tidal rise), sometimes against mangrove stems (Abraham, 1924), are probably in effect arboreal foragers.

However, until recently there was no known example of an Australian mygalomorph which fed in the foliage or canopy of vegetation. Therefore, the turret-building species of *Aname* is of interest. The tubes open either in gaps amongst the foliage or above the canopy of tussocks and shrubs. The spiders presumably do not venture far, if at all, away from the entrance (and are unlikely to crawl down the outside of the tube to the ground) and thus are dependent on insects creeping amongst and on the foliage and flying insects as they alight. This would mean that they are a truly foliage or canopy forager as distinct from arboreal spiders which forage on the trunks of trees and shrubs.

BURROW MODIFICATIONS AS A RESPONSE TO HISTORICAL ENVIRONMENTAL CHANGES

The arboreal tubes and most corticolous nests in mesophytic and rainforest habitats have evolved *in situ* in continuously humid habitats (but where some sites may experience extreme flooding). In contrast, of those flood-adapted nests which occur now in semi-arid and arid habitats most have evolved (*in situ*) from mesophytic denizens but as a result of a general drying of the habitat associated with climatic aridification. Paradoxically while probably making simple tubes and burrows in a "primitive", uniformly wet habitat the spiders have been exposed to the the hazard of sheet flooding as a result of periodic deluges associated with a dryer, but seasonal climate. Nevertheless, clearly a few such species do belong to taxonomic groups which already had burrows and doors well adapted to sudden deluges in rainforest and mesophytic habitats, e.g., species of *Arbanitis*.

Much of the semi-arid woodland, shrubland and saltbush steppe of southern Australia enjoyed a consistently wet climate and supported mesophytic forest and rainforest interspersed with swampland during the early Tertiary (Cookson, 1973; Cookson & Pike, 1953, 1954; Truswell, 1990). With progressive drying of the climate and development of a markedly seasonal weather pattern the vegetation was altered, leaving some relictual, moist microhabitats in juxtaposition with other seasonally alternating wet/dry microhabitats some of which now experience periodic, sudden inundation.

Certain species of trapdoor spiders whose taxonomic relatives in rainforest and mesophytic habitats lack specialised burrow structures have responded to seasonal sheet flooding in arid habitats by modifying burrow structures in flood avoidance. Notable types of burrow modification in the western part of the continent, which are hypothesised as having evolved in direct response to (geologically) historical changes in the environment are the burrows of *Aganippe castellum*, *Teyl* species with both surface and subterranean doors and the aerial tubes of the *Aname* species. Main (1986) discussed the probable origin of the semi-arboreal nest of *A. castellum*, its anti-flooding function and adoption of a 'new' foraging behaviour. This dual adaptation probably evolved during the late Miocene/Pliocene in response to fluctuating wet/dry seasons and fragmentation of the landscape into a mosaic of wet and dry microhabitats. It also has been postulated earlier (Main, 1976) that the single surface door of some *Teyl* species evolved in response to climatic/habitat changes towards a seasonal weather regime and more open habitat. The turret nest of the *Aname* species has probably, similarly developed contemporaneously, in response to the drying of the climate, in different geographic habitats but which also occur in areas subjected to some seasonal, torrential or at least very heavy rain which causes flash flooding.

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INTRASPECIFIC PREDATION IN *CLUBIONA CORTICALIS* (ARANEAE: CLUBIONIDAE)

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Marc, P. 1993 11 11: Intraspecific predation in *Clubiona corticalis* (Araneae: Clubionidae). *Memoirs of the Queensland Museum* 33(2): 607-614. Brisbane. ISSN 0079-8835.

Clubiona corticalis is supposed to be a useful biological control agent of lepidopteran larvae (e.g. Tortricidae) in orchards. Thus, the levels of its intraspecific predation especially when bred in captivity must be determined. Predation is a risk at mating and dispersal. Cannibalism during mating, studied at 13°C, 20°C and 27°C and without prey in cages, remains low (1.5%) during the first 24 hours at all temperatures. After 24 hours cannibalism increased and was significantly higher at 27°C than at 13°C after one week. Males were 72% of the victims. Males can mate twice with different without increasing the risk of cannibalism. The spiders were studied for 12 days after dispersal. Until Day 3, no intraspecific predation occured, whatever the availability of prey for juveniles. Intraspecific predation is very much reduced by the availability of sufficient prey, and a female given prey did not feed on its own progeny. *Clubiona corticalis* pourrait être utilisée en verger pour lutter contre des larves de lépidoptères (Tortricidae). Il était donc important de connaître les niveaux de prédation intraspécifique chez cette espèce, lorsqu'elle est élevée en captivité. Il est montré qu'il y a des risques de prédation à deux moments du développement: l'accouplement et la dispersion. Le cannibalisme durant l'accouplement, étudié à 13°C, 20°C et 27°C sans proie dans les enceintes, reste faible à toutes les températures (1.5%) pendant les premières 24 heures. Après 24 heures, le cannibalisme augmente. Il est significativement plus fort à 27°C qu'à 13°C après une semaine. Les mâles sont les victimes dans 72% des cas et peuvent s'accoupler deux fois avec des femelles différentes sans augmenter les risques de cannibalisme. Les jeunes araignées sont étudiées pendant douze jours après la dispersion. Quelle que soit la disponibilité en proies, aucun cas de prédation intraspécifique n'intervient jusqu'au troisième jour. Ensuite, la disponibilité en proies dimunue de façon très significative le niveau de canabalisme. A noter qu'une femelle disposant de proies, n'exerce aucune prédation sur sa progéniture.□*Biology, Europe, laboratory, Araneae, France, breeding, auxiliary, intraspecific predation, Clubiona corticalis, dispersal, mating.*

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Clubionids are wandering, nocturnal spiders (Marc, 1990a), and certain species are efficient in caterpillar control in orchards (Mansour *et al.*, 1980; Marc and Canard, 1989). The study of the arachnofauna in apple orchards led us to take an active interest in whether *Clubiona corticalis* (Walckenaer) can be used in biological control of pest caterpillars. In the laboratory, all instars of *C. corticalis* can consume large quantities of lepidopteran larvae, especially tortricids, harmful to orchards (Marc, unpublished data). However, the efficacy of using *C. corticalis* in biological control remains uncertain. Spiders are generally envisaged as having high rates of intraspecific and interspecific predation (Bristowe, 1958; Greenstone, 1978). If this is true for *C. corticalis*, then its effectiveness in biological control would be reduced, i.e., an increase in spider densities in the field would increase cannibalism. Thus, data on rates of cannibalism in *C. corticalis* are needed.

In *Anyphaena accentuata* (Walckenaer), *Philodromus cespitum* (Walckenaer) and *Diaea dorsata* (Fabricius) (the most abundant non-web spinning spiders in apple orchards), intraspecific and interspecific recognition minimizes cannibalism (Marc, 1992). Whether this is true of *C. corticalis* is not known. *C. corticalis* occurs in very high densities on pines (Marc, 1990b) where they build silk nests under bark for refuge during the day (Marc, 1990a). Partially flaking bark are favoured shelters on which concentrations of 6-12 nests can be found in 10-15cm^2 (often the clustered nests are stuck together). Furthermore, nests of other clubionids, *Clubiona brevipes* Blackwall, *C. leucaspis* Simon and *Ceto laticeps* (Canestrini), often adjoin those of *C. corticalis*. These aggregations suggest low intraspecific and interspecific predation in nature. However, laboratory bred spiders for use as auxiliaries may present special problems. In captivity, intraspecific predation at critical moments of develop-

ment may be artificially high because contact between individuals is more frequent. Mating and dispersal are likely to be critical periods (Fig. 1). This work determines levels of cannibalism in *C. corticalis* when bred in captivity.

MATERIALS AND METHODS

Subadult spiders (one instar before maturity) were collected in winter, in a forest under the bark of *Pinus sylvestris*. Removed from the field in Ependorff micro-tubes, they were separated into males (recognisable at this instar by a bulging palpal tarsus) and females. Each individual was then placed in Petri dishes (9 cm in diameter and 1.5 cm high) for breeding. Damp cotton wool kept humidity high in cages. Individuals were fed with two flies (*Lucilia*, Diptera) three times per week. Unless otherwise specified all procedures and observations where carried out in the laboratory. All enclosures are here referred to as 'cages'.

Cannibalism during Mating

In each of 135 Petri dishes, one male was placed with a virgin female, and no food was added for the week of the experiment. Breeding cages were kept at 13°C, 20°C and 27°C under long photoperiod (L-D=16-8), and were observed several times a day. Males and females used for mating had all moulted to adults at least two weeks before.

Cannibalism After Dispersal

Dispersal, in this species, is when the juveniles at instar 2 leave the female's breeding-nest. Cannibalism, from dispersal (when the first juvenile leaves the breeding-nest) for 12 days was observed on eight egg masses from mating carried out. The egg masses were inside the female's cages (25ml Petri dishes). These observations were carried out at 20°C and in a L:D photoperiod of 16:8. Two groups of 4 egg masses each were set up:

- no prey for the juveniles. In two cages the female had been separated from her progeny.
- *Drosophila* provided for juveniles. The female was taken out of one dish.

Lucilia were given to the females left in the cages every day from the second day after the dispersal of the first of the juveniles. The caged spiders were observed 2-3 times a day for 12 days and the status–alive, death by cannibalism, or death by other causes, or still inside the nest–recorded.

RESULTS AND DISCUSSION

Cannibalism during Mating

In the final moult the reproductive organs are completely formed. Trophic, and locomotory activities and very different behaviour in two sexes of the *C. corticalis* species also appear (Marc, 1992). In the field, males become adults about 10 days before females (Marc, unpublished data). Males then seek females, inside whose nests mating takes place. Because of this asynchrony of maturity, males frequently mate with females soon after the latter moult and at which time females do not feed; they remain in their nest without feeding for 1-2 days after moulting (Marc, 1990a). These two days appear, therefore, to be an especially favourable time for the male to mate because, during this time, the female is only slightly aggressive. Males may also build a nest adjoining those of the subadult females and thus fertilise them soon after the final moult. This was also observed by Austin (1984) in *C. robusta* L. Koch and by Wolf (1990) in *Cheiracanthium pennyi* Cambridge and *Cheiracanthium punctorium* (Villers). The mating of many other species takes place just after the final moult of females. Jackson (1980a) reported that 161 species use tactics of cohabitation (the male stays with the immature female to mate with her after she has undergone her adult moult).

Here, successful mating could be obtained several weeks after the final moult of both sexes. The male approaches the female by tapping on her nest. Copulation, which takes place inside the female's nest, lasts for about 3 hours. The male, mounted on the female's back and facing the same direction, forms an angle of about 45° to her. From this position, he applies each palp consecutively into her epigyne. One male can fertilize the eggs of at least 3-4 females. Mating can also take place outside the female's nest without cannibalism. On the other hand, in other species, intraspecific interactions outside the nest were more 'lethal' (Jackson, 1988a; Jackson and Macnab, 1989).

Intraspecific predation was observed in 13% of the cases for all matings (Fig. 2). The most favourable conditions to reduce the risks of cannibalism during mating would have been to place the males in the female's cages just after the female's moulted, or, at least, in the presence of prey. Yet, here, males were brought to females which had moulted at least 15 days before. Furthermore, no food was provided. Because, to be practicable for production of auxiliary popula-

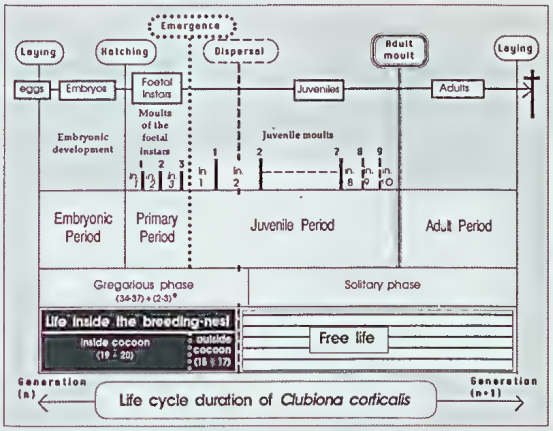

FIG. 1. Life cycle of *Clubiona corticalis*. Terminology in Canard (1987). *In.1*, *in.2* and *in.3* indicate the foetal instars, and in.1 to in.10 the juvenile ones (last juvenile instars, 9 and 10, not present in every individual). Numbers in parentheses indicate duration in days. * (2-3) refer to Time spent by juveniles close to breeding-nest just after dispersal.

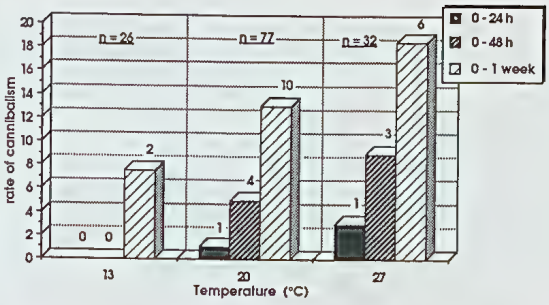

FIG. 2. Intraspecific predation rate during mating experiment on *C. corticalis* without prey at 13, 20 and 27°C. Symbols indicate the period of predation; n = no. of pairs tested; values on histogram bars =no. cases recorded.

tions for biological control, the time needed for care during laboratory breeding must be minimal. Synchronized mating was more practicable. Likewise, the absence of prey in the mating cages simplifies the work. Cannibalism observed after one week (13%) was very much higher than that in the field.

Predation before 24 hours, whatever the temperature, were rare (1.5%) (Fig. 2), but thereafter increased with time and after one week the rate of cannibalism was significantly lower (p) at a lower temperature (7.5% at 13°C and 18.5% at 27°C).

The spider's activity is probably related to the temperature. Indeed, locomotory activity increases with temperature and greatly increases the probability of interindividual encounters and, therefore, the risks of aggressiveness, especially in the absence of prey.

Cannibalism in 24 hours was rare, whatever the temperature, even though the trophic needs of females, especifically after adult moulting, must be high considering ovule production. This can be explained simply by the smaller need for food after only one day of fasting, when this time is sufficient to guarantee mating. Indeed, the pairing time was quite short. Within 5 hours of the individuals being brought together, 75% of the matings had begun, and mating itself lasted 3 hours. We observed, however, that one male could mate several times with the same female which lengthens the interaction, but it seems that this has no effect on the number of egg masses or on the descendants produced by the female. At 13°C no intraspecific predation occurred before 48 hours, and the females were fertilized normally and laid fertile eggs in the same way as at 20°C and 27°C.

In all pairs where intraspecific predation occurred once in the week after the start of the experiment, males are more often (72%) the victim. We did not observe a relation between weight and the individuals eaten, and sometimes smaller individuals ate larger ones. There is no significant sexual dimorphism in *C. corticalis*.

In contrast, even though size is not important, males do move more than females (Marc, 1990a). Conceivably, this weakens males relative to similar sized females. Furthermore, males who have smaller trophic needs and mate several times with different females display less aggressiveness towards their partners. This may partly explain why males were more often the victims of cannibalism.

A male can mate once or twice without significantly increasing the rate of cannibalism after one week (9% for one mating and 14% for two matings; $p>0.05$). However, after two further matings (3 or 4), intraspecific predation increases significantly to 33% ($p<0.05$) if compared to a male which mated only once. However, the male is not always the victim.

In *C. reichlini* Schenkel, males and females can mate several times without cannibalism (Hengmei and Hongquan, 1987). Equally, in interactions of *C. cambridgei* L. Koch, no cannibalism occurred between virgin males and females during the 38 interactions studied (Pollard and Jackson, 1982). Generally, species of *Clubiona* do not seem to be very aggressive

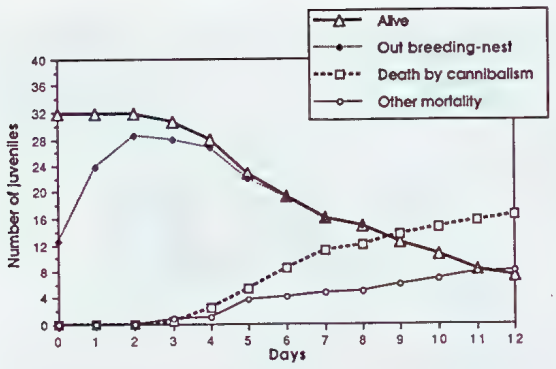

FIG. 3. Survival of juveniles (2nd instar) of *C. corticalis* during 12 days after dispersal, without prey.

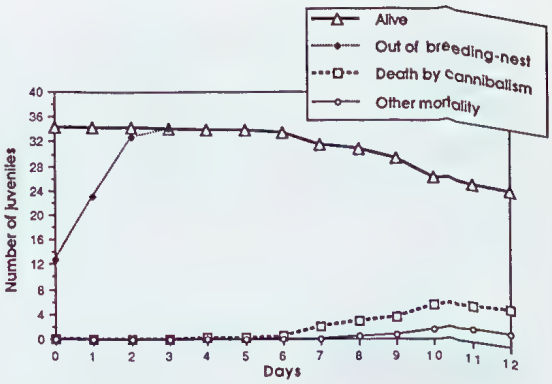

FIG. 4. Survival of juveniles (2nd instar) of *C. corticalis* in the presence of prey.

toward each other during mating. Apparently, to eliminate cannibalism in *C. corticalis*, males and females should be brought together at about 13°C and individuals should be kept paired for about 24 hours. Furthermore, the presence of prey at 13°C should make the cohabitation of males and females perfectly feasible for several days without intraspecific predation occurring. Such conditions during mating should minimize the manpower needed and lower production costs.

Cannibalism After Dispersal

Juveniles leave the breeding-nest, built by the female, after 1-4 days. Then, they remain grouped around the nest for about 2-3 days before dispersal. This gregarious phase lasts 17-20 days at 20°C (15-17 days in the breeding-nest and 2-3 days around the nest) (Fig. 1). It is only from the juvenile instar 2 (as defined by Canard, 1987), that juveniles begin to hunt. Until leaving the breeding-nest juveniles use on their vitelline reserves and, some attack the undeveloped eggs in the nest. Indeed, weight differences between juveniles leaving the breeding-nest indicate the existence of trophic activity in some individuals, as there are no significant weight differences known to occur between eggs in the same batch in the spider (Lecaillon, 1905). Furthermore, this trophic activity does not seem linked to the female feeding her juveniles by regurgitation or the consumption by the juveniles of a trophic egg-mass as, for example, in *Amaurobius* (Amaurobiidae) (Tahiri *et al.*, 1989). At this point, mortality is the highest in many species (Austin, 1984). It may be even more delicate in a captive breeding situation as the juveniles, in large numbers in the cages, would devour each other.

The dispersal of the juveniles given prey can spread over 4 days (Fig. 3). There was no significant difference between the cages with a female and those with one removed ($p>0.05$). Thus, females did not attack their own progeny after dispersal for at least the first 12 days and on the condition that prey was available. Cannibalism between the juveniles first began 3-4 days after the first dispersal and coincided with the expression of the first agonistic behaviour observed. Next, the number of juveniles decreased until there are about 10 individuals per cage towards the eleventh day.

When the juveniles were fed *Drosophila* (Fig. 4), the female's influence on this period of her progeny's development was similar. On the other hand, intraspecific predation was almost non-existant in the first 6 days and continued to be minimal afterwards, being about 5% after 10 days. There is a highly significant difference between the two groups after the 12 days of study ($p<0.001$). Thus, with prey in the breeding cage, cannibalism decreased and was almost eliminated. Rypstra (1983), likewise, found in several spider species that intra-individual tolerance increased and cannibalism decreased when maintained at extremely high prey levels. Also, Krafft *et al.* (1986) were able to prolong the juvenile social period by giving juveniles abundant food. Austin (1984) recorded a high mortality in the breeding of *C. robusta*, cannibalism being one of the two major causes of mortality. On the other hand, in nature, spiders, which are potential prey of the highest density in the environment, only represented only 3% of prey actually consumed (Austin, 1984). Austin suggested that the highest mortality occurs at the dispersal instar.

The rest of the development presents fewer

Fam	Genus or species	Authority
Club	*Supunna picta*	Jackson & Poulsen (1990)
Gnap	*Taieria erebus*	Jarman & Jackson (1985)
Liny	*Oedothorax insecticeps*	Kiritani *et al.* (1972)
Lyco	*Lycosa pseudoannulata*	Kiritani *et al.* (1972)
	Pardosa lugubris	Edgar (1969)
	P. purbeckensis	Schaefer (1974)
	P. ramulosa	Yeargan (1975)
	Pirata piraticus	Schaefer (1974)
Mime	*Ero aphana*, E. furcata**	Gerhardt (1924), Bristowe (1941), Czajka (1963), Canard (1984)
	Mimetus maculosus, M.* sp.*	Jackson & Whitehouse (1986)
Oxyo	*Peucetia viridans*	Turner (1979)
Phol	*Holocnemus pluchei*	Blanke (1972)
	*Pholcus phalangioides**	Jackson & Brassington (1987), Jackson & Rowe (1987)
Salt	*Brettus adonis°*, B. cingulatus°**	Jackson & Hallas (1986a)
	Cocalus gibbosus	Jackson (1990b)
	Cobanus mandibularis	Jackson (1989)
	*Cyrba algerina°**	Jackson & Hallas (1986a)
	*C. ocellata°**	Jackson (1990c)
	Euryattus sp.	Jackson (1985a)
	Gelotia sp.°*	Jackson (1990d)
	Jacksonoides queenslandica°	Jackson (1988a)
	Phaeacius malayensis, P. sp.	Jackson & Hallas (1986a), Jackson (1990a)
	Plexippus paykulli	Jackson & Macnab (1989)
	Phidippus johnsoni	Jackson (1977)
	*Portia°**	Jackson & Hallas (1990)
	*Portia fimbriata°**	Jackson (1982a, 1986b), Jackson & Blest (1982), Jackson & Hallas (1986b), Jackson & Wilcox (1990)
	P. africana°, P. albimana°**	Jackson & Hallas (1986b)
	P. labiata°, P. shultzi°**	Jackson & Hallas (1986b)
	Simaetha paetula	Jackson (1985b)
	Tauala lepidus	Jackson (1988b)
Scyt	*Scytodes longipes*	Nentwig (1985)
Ther	*Achaearanea camura*	Jackson (1988b)
	Achaearanea tepidiorum	Rypstra (1986)
	Rhomphaea	Enders (1974)

TABLE 1: Literature review of araneophagic spiders: species principally or strongly araneophagic. *, 'aggressive mimicry' = to perform a variety of vibratory behaviour in which the prey-spider responded as it normally would to its own prey. °, oophagy.

problems of cannibalism. Six groups of juveniles were bred together with 5 per Petri dish from instar 2-6 and no cannibalism was noted. Furthermore, the periodic absence of prey during a few days (3-5) in the cages did not result in intraspecific predation, but behaviour of escape and avoidance was observed. Similar observations had been made on sub-adults and adult females bred at 25-30 individuals per cage (30×20×20 cm) over 2 months.

Family	Genus or species	Authority
Anyphaenidae	*Anyphaena accentuata*	Marc (1992)
Heteropodidae	*Olios diana*[k]*, O. lamarcki*[k]*, O. obesulus O.* sp.[k]	Jackson (1987)
Hexathelidae	*Porrhothele antipodiana*	Jackson & Pollard (1990)
Philodromidae	*Philodromus cespitum*	Marc (1992)
Salticidae	*Holoplatys* sp.	Jackson & Harding(1982)
	Myrmarachne lupata	Jackson (1982b)
Thomisidae	*Diaea dorsata*	Marc (1992)

TABLE 2: Literature review of araneophagic spiders: species which are little or not araneophagic. [k], species kleptoparasitic which are not araneophagic.

Therefore, in breeding *C. corticalis*, the provision of *Drosophila* to juveniles at the dispersal stage should be sufficient to eliminate intraspecific predation. Then, 5 days after dispersal when all juveniles are out of the breeding-nest and no cannibalism has occured, the division of these juveniles at instar 2 with about 5 per Petri dish, should prevent cannibalism later.

CONCLUSIONS

Intraspecific predation in *C. corticalis* during two especially susceptible periods of development (mating and dispersal) involves limited risks of cannibalism which can be eliminated. Mating must be at 13°C. Males in the enclosures with females must be limited to 24 hours, and dispersing juveniles must have sufficient prey. Cannibalism should not, therefore, be an obstacle to the mass breeding of this species for biological control.

Rates of intraspecific and interspecific predation have often been considered very high in spiders. The main enemies of spiders are often other spiders (Bristowe, 1941; Foelix, 1982). Certain species partially practice araneophagy (e.g. *Pardosa lugubris* (Walck-enaer), *Lycosa annulata* Thorell), and a few make it their speciality (e.g. *Mimetus*, *Ero*, *Portia*) (Table 1). In fact, the species most studied for cannibalism are araneophagic in nature. In contrast, in other species, araneophagy appears to be almost non-existant (Table 2) even without prey (e.g. *Anyphaena accentuata*, *C. corticalis*, *Diaea dor-*

sata, Philodromus cespitum) and it is absent in social spiders such as *Mallos gregalis* (Simon) (Jackson, 1979, 1980). Behaviour of a few spider species cannot be applied to all. The degree of araneophagy of a species must be based on only that one. Therefore, the levels of intraspecific and interspecific predation amongst the more abundant species in agrosystems in which a spider is a possible biological control agent must be studied. A simple method has been finalised for spiders which do not spin a web (Marc, 1992).

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COMPARATIVE MORPHOLOGY OF THE SEXUALLY DIMORPHIC ORB-WEAVING SPIDER *ARGIOPE BRUENNICHI* (ARANEAE: ARANEIDAE)

MONIKA C. MÜLLER AND WILFRIED WESTHEIDE

Müller, M.C. and Westheide, W. 1993 11 11: Comparative morphology of the sexually dimorphic orb-weaving spider *Argiope bruennichi* (Araneae: Araneidae). *Memoirs of the Queensland Museum* 33(2): 615-620. Brisbane. ISSN 0079-8835.

Although the web building spigots of the glandulae aggregatae and the glandulae flagelliformes are not functional in mature males, adult *Argiope bruennichi* and *A. lobata* males are able to build webs. The structure of these webs is described. The aciniform spigots on the intermediate spinnerets of *A. bruennichi* males have degenerated to a great extent. Culture experiments with *A. bruennichi* enabled us to follow differences in the development of female and male morphology. The presence of the tubuliform spigots in the sixth instar suggests one possible evolutionary hypothesis concerning sexual dimorphism in spiders.
Nach der Reifehäutung sind die aggregaten und flagelliformen Spulen–welche als Triade die Fangfäden sezernieren–auf den hinteren Spinnwarzen der Männchen nur rudimentär ausgebildet. Trotz dieser Reduktion spannen adulte *Argiope bruennichi* und *A. lobata* Männchen Radnetze, deren Struktur beschrieben wird. Auf den mittleren Spinnwarzen subadulter und adulter *A. bruennichi* Männchen ist ein hoher Prozentsatz der aciniformen Spulen unvollständig ausgebildet. Durch Aufzucht der Wespenspinne war es möglich, morphologische geschlechtsspezifische Unterschiede in der Postembryonalentwicklung festzustellen. Das frühe Auftreten der tubuliformen Spulen im weiblichen Spinnapparat kann als Argument für eine Hypothese zur Evolution des Sexualdimorphismus interpretiert werden. □% *Development, sexual size dimorphism, spinning apparatus, male orb-webs, tubuliform spigot.*

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Sexual dimorphism varies across taxa, but the question of whether highly dimorphic species occur as a result of selection for large female or small male size remains controversial.

Gerhardt (1924) observed that both carnivorous feeding habits and cannibalism endanger male spiders before, during and after copulation (Elgar and Nash, 1988). Darwin (1890) and Bristowe (1929) suggested that their small size protects the males from the females which do not recognize males of reduced size as prey. In contrast, Gerhardt (1924) and Vollrath (1980) argue that 'the females have evolved to be larger, allowing greater egg production' (Vollrath, 1980: 165).

Morphological investigations of sexual size dimorphism are rare; for example Sekiguchi (1955a, b) compared the spinning apparatus in male and female spiders. The present investigation examines whether or not there are morphological data that could be used to assess these different ideas, by analysing the spinning apparatus in different instars of *Argiope bruennichi*.

MATERIALS AND METHODS

Adult males and females of *Argiope bruennichi* (Scopoli, 1772) were collected from Dabas (Hungary), and subadult males and cocoons from Wittenberg-Lutherstadt (Germany).

Specimens of *A. bruennichi* were raised individually from the third instar. Some individuals from each instar were fixed in Carnoy's fluid immediately after moulting. The lengths and widths of the prosoma were measured. For SEM studies the spinning apparatus was removed and the spinnerets were dehydrated in ethanol and critical point dried with carbon dioxide. After sputtering with gold, they were analysed with a Cambridge Stereoscan 250. For light microscopy the spinnerets were separated into smaller pieces and embedded in Swann-fluid.

Subadult males of *A. bruennichi* were kept in plexiglass frames from the penultimate stadium until they died.

Early instars were fed with greenflies (Aphidina) and *Drosophila melanogaster* while older stages were provided with various insects captured in the field.

RESULTS

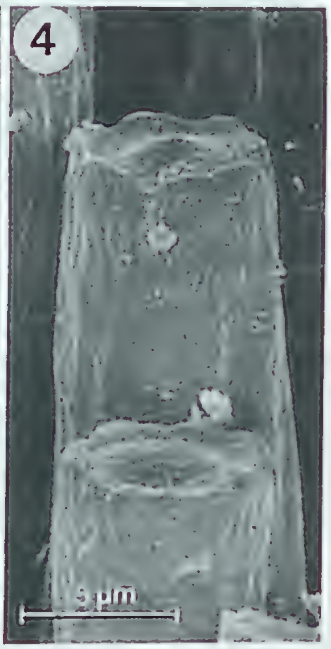
ADULT *ARGIOPE* MALES CAN SPIN WEBS

The posterior spinnerets of adult males are

1
ags
fs
ags
20 µm

2

3
50 µm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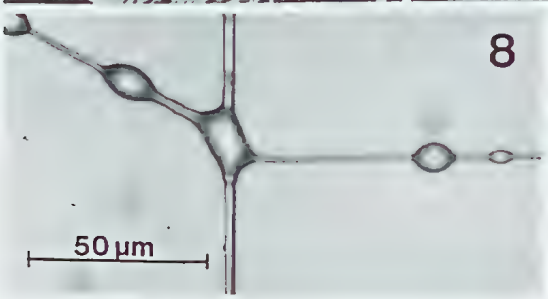
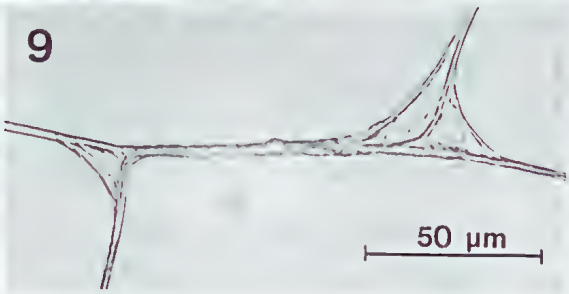

8
50 µm


9
50 µm

equipped only with rudimentary projections of the triad spigots (Fig. 1). These aggregate and flagelliform spigots–which usually furnish the capture threads–obviously do not function. Nevertheless, adult males of *A. bruennichi* and *A. lobata* spun rudimentary orb-webs (Fig. 2). These webs were destroyed every day during our study and the spiders renewed them almost daily. Subadult males spun normal orb-webs with the typical stabilimentum until the last moult. Webs spun after the terminal moult were smaller than subadult webs. They showed an irregular structure; but radia and a spiral were present. This spiral consisted of a few turns with remarkably increasing space outwards thus showing a closer resemblance to the auxiliary spiral than to the capture spiral. No droplets adhered to the spiral threads when the spiders were sprayed with water using an atomiser. They seemed to be thinner than capture threads and were not sticky. Prey thrown into the webs did not adhere to the spiral threads. A microscopical investigation revealed that their structure also strongly resembled auxiliary threads (Figs 5-7). The auxiliary nature of the web was confirmed by comparing the connection points of different types of threads with the radia (Figs 8-9).

Intermediate Spinnerets of Adult Males

The number of piriform and aciniform spigots for each sex were counted under the light microscope. There were fewer bases than apical parts of the aciniform spigots in the intermediate spinnerets of males. SEM examinations showed that a surprisingly high number of apical parts were degenerated (Figs 3-4). Only 19.2% (6 individuals) of the aciniform spigots on the intermediate spinnerets were fully developed. This degeneration was less in subadult males.

Postembryonic Development of Body Size

The shape of the opisthosoma changed during the development of *A. bruennichi*. The spherical form changed into an elongated one, reaching the proportion of adult spiders at the sixth instar. This pattern is clearly shown by the length/width-quotient of the opisthosoma in each instar (see Table 1). The development of both prosoma and opisthosoma was nearly uniform for all individuals until the sixth instar, although the intervals between the moults varied (instar III to IV: 17-73 days; instar IV to V: 11-52 days). Following the sixth instar (when subadult males could be first determined) the sexes developed differently (Fig. 15). This pattern of development of sexual dimorphism is less apparent in the prosoma.

	II	III	IV	V	VI	VII	VIII	♂	♀
	1.3	1.4	1.4	1.6	1.9	1.8	2.0	1.9	1.9
S.D.	0.09	0.08	0.04	0.09	-	-	-	0.14	0.56

TABLE 1. *Argiope bruennichi*. Length/width-quotients and standard deviation of the opisthosoma for different instars (II-VIII) and adults (n = 62).

Postembryonic Development of the Spinning Apparatus

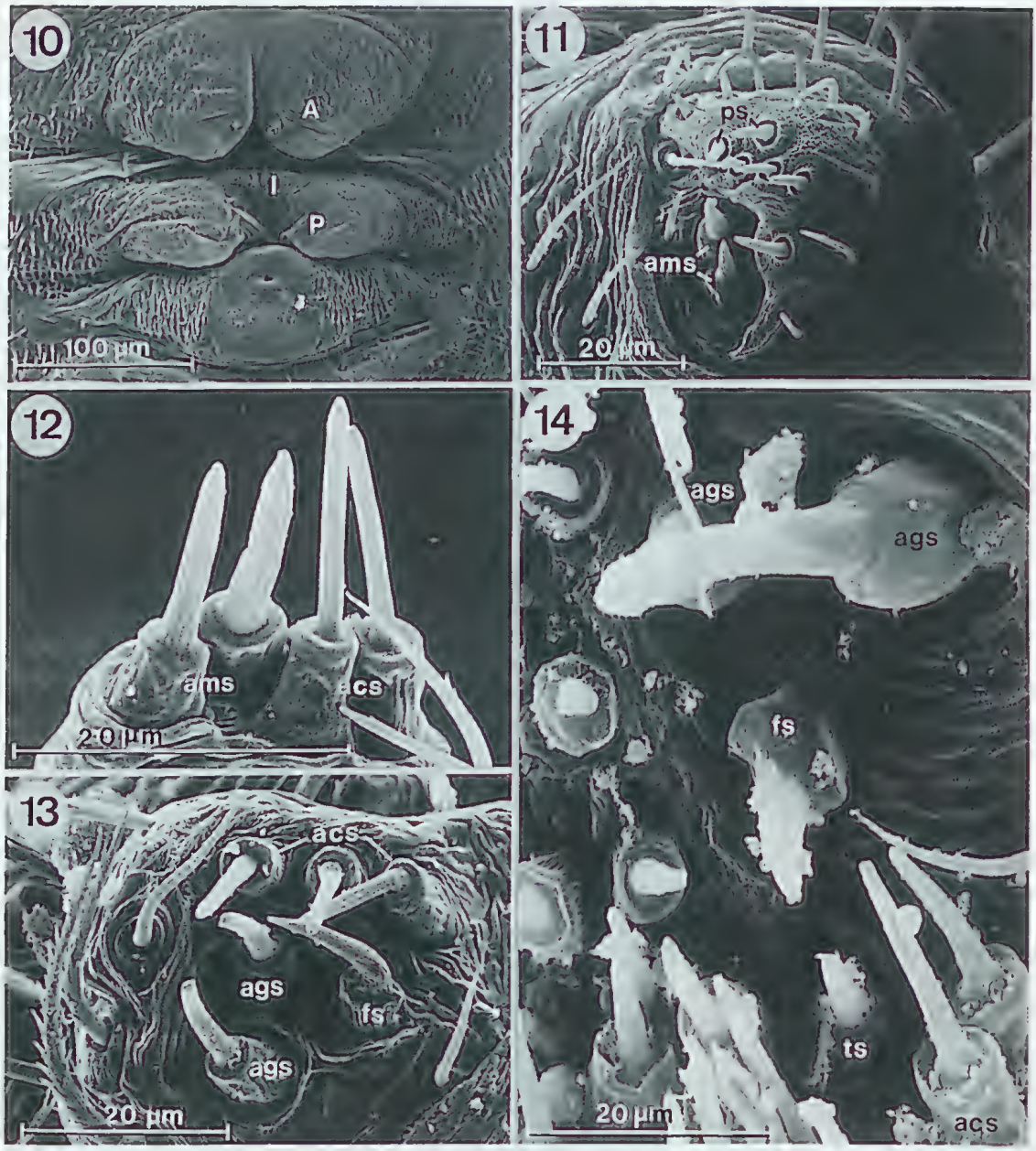
The development of the spinnerets was documented by counting the piriform and aciniform spigots. None of these fusules was found in the second instar (Fig. 10). Six piriform (anterior spinnerets), two aciniform (intermediate spinnerets) and three aciniform spigots (posterior spinnerets) were counted for third instar individuals (Figs 11-13). The development of the spigot number was uniform until the sixth instar. From that stadium on, the sexes developed differently as shown for the aciniform spigots on the posterior spinnerets (Fig. 16). Although the anterior and intermediate spinnerets develop in the same way (Fig. 16), the differentiation of the sexes is less obvious.

Tubuliform spigots were also first observed in the sixth instar of female spiderlings (Fig. 14).

DISCUSSION

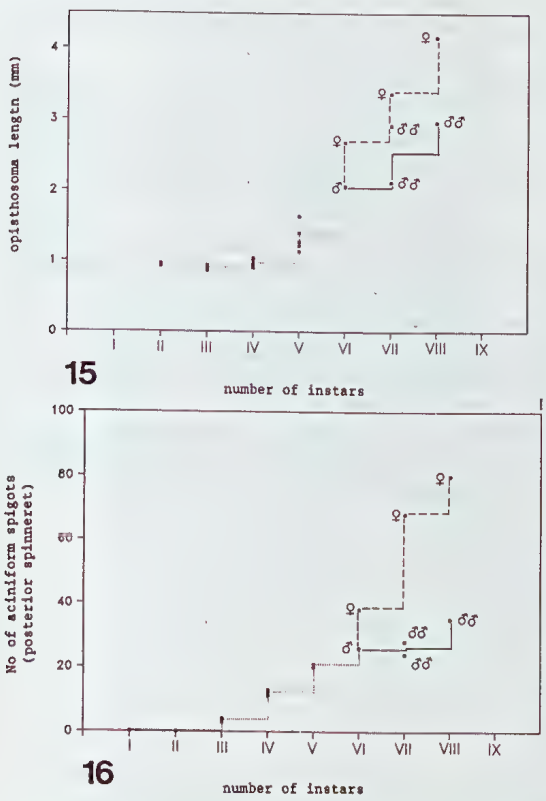
The degeneration of the triad spigots on male posterior spinnerets during the terminal moult was first described by Sekiguchi (1955b) and subsequently documented for other species. These morphological reductions in males were explained by changes in their behaviour: adult males cease spinning webs and instead search for females. Emerton (1878) and McCook (1890) mentioned that small webs were spun by *Argiope aurantia* males, but no information about the structure of these webs was provided. This study shows that *A. bruennichi* and *A. lobata* males are capable of spinning webs. The spiral threads of

FIGS. 1-9. 1. Triad spigots at posterior spinneret of adult male. Apical parts of aggregate (ags) and flagelliform (fs) spigots missing, bases vestigal. 2. Orb-web of adult *Argiope bruennichi* male. 3. Intermediate spinneret of adult male. Many apical parts of aciniform spigots missing. 4. Detail of 3. 5-9. Different structures of male webs. 5: Capture thread (subadult male); 6: Auxilliary thread (subadult male); 7: Spiral thread (adult male); 8: Junction of a capture thread with a radia; 9: Junction of a spiral thread with a radia.



FIGS 10-14. Developmental stages of spinning apparatus. 10: Second instar; anterior (A), intermediate (I) and posterior spinnerets (P) are undeveloped; 11-13: Third instar; 11: Anterior spinneret with six piriform (ps) and two ampullate (ams) spigots; 12: Intermediate spinneret with two aciniform (acs) and two ampullate (ams) spigots; 13: Posterior spinneret with three aciniform spigots (acs) and the triad (consisting of two aggregate (ags) and one flagelliform (fs) spigots; 14: Detail of posterior spinneret of ♀spiderling at sixth instar. Tubuliform spigot (ts) is clearly to differentiate from aciniform spigots (acs). Note arrangement of triad: aggregate (ags) and flagelliform (fs) spigots stay apart from each other, typical for subadults.

these webs resemble auxiliary threads, and therefore are not furnished by the triad glands which still exist immediately after the last moult (see Sekiguchi, 1955b). The auxiliary thread type was recognized because the threads were not covered with glue droplets. However, it is possible that these threads are not auxillaries: Vollrath and Edmonds (1989) found that the glue is soluble in



FIGS 15-16. Postembryonic development of *Argiope bruennichi*: 15: Opisthosoma length; 16: Number of aciniform spigots at posterior spinneret.

water and Peters and Kovoor (1991) argue that the glue does not necessarily fall into droplets.

It is not clear why adult males produce these rudimentary webs, but their poor design suggests that it is unlikely that they function to catch prey. That adult males rejected food offered with tweezers can support this assumption.

The females in spider genera that exhibit extreme size dimorphism are usually hemisessile. Thus courtship and mating is achieved by male mobility. Male mobility is achieved by using bridging lines and ballooning (Peters, 1990). McCook (1890) described these balloon lines as consisting of quite a number of threads that remain separated from one another, which suggests that they are furnished by the aciniform spigots. The degeneration of these aciniform spigots on the intermediate spinnerets of adult *Argiope bruennichi* males may occur because the remaining spigots are sufficient to produce the balloon lines. Alternatively, these threads may originate from other spigots. If the aciniform spigots of the posterior spinnerets furnish the balloon lines, then their degeneration on the intermediate spinnerets would not disadvantage the males. Since adult males do not depend on the additional function of the aciniform threads (in terms of prey wrapping) their degeneration may be interpreted as a morphological adaptation to an altered style of life.

These results suggest that the development of sexual dimorphism takes place in the sixth instar.

Townley *et al.* (1991) reported tubuliform spigots in *Araneus cavaticus* in the fourth instar, which is equivalent to the sixth instar of *Argiope*. Townley *et al.* (1991) suggested that the tubuliform spigots are present that early in order to 'stake out sites for the functioning spigots of mature females, because the tubuliform glands are poorly developed and do not serve any function at that time'. This explanation seems unlikely because the spinnerets are reorganized and the number of fusules increases with each moult.

In contrast, we consider the existence of the tubuliform spigots already at the sixth instar in female spiderlings to be an indication for the hypothesis that phylogenetically earlier females reached maturity at this developmental stage.

In females the tubuliform spigots may indicate the penultimate stadium as do the swollen palpi in males. While the males become mature, females undergo another series of moults (3-4) to reach maturity. During their phylogenetic history, the females in the subadult stage–more exactly in the penultimate stadium–undergo a prolongation of their development resulting in a larger body size, directly correlated with higher egg production. Therefore, sexual size dimorphism may have evolved to produce larger females, a hypothesis as especially presented by Gerhardt (1924) and Vollrath (1980).

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A METHOD TO DEVELOP AN 'INDICATOR VALUE' SYSTEM FOR SPIDERS USING CANONICAL CORRESPONDENCE ANALYSIS (CCA)

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Multivariate Canonical Correspondence Analysis (CCA) is used to derive 'indicator values' for spiders, similar to those used for plants. The data set consists of activity abundance values of spiders, sampled by pitfall trapping in various habitat types (mires, woods, dry grassland) in the Berlin area. Light exposure, soil moisture and temperature were also measured at the sites. Species scores are plotted as a function of environmental factors within an ordination diagram. The method used to determine the indicator value from this ordination diagram is presented. The system of indicator values is regarded as a suitable method to evaluate sites and areas easily. Advantages and limitations are discussed.

Mit Hilfe der multivariaten statistischen Methode Kanonische Korrespondenz Analyse (CCA) werden Zeigerwerte für Webspinnen, ähnlich denen für Pflanzen ermittelt. Die Entwicklung dieses Zeigerwertsystems und dessen Anwendung wird im Prinzip beschrieben. Der verwendete Datensatz besteht aus Aktivitätsabundanzwerten von Spinnen, die mit Bodenfallen in unterschiedlichen Biotoptypen (Mooren, Wäldern und Trockenrasen) im Gebiet von Berlin gefangen wurden. Die an den Standorten gemessenen abiotischen Faktoren Licht, Temperatur und Bodenfeuchte werden mit in die CCA einbezogen. An Hand von Beispielen wird der Weg erläutert, Zeigerwerte aus Ordinationsdiagrammen zu ermitteln. Mit Hilfe einiger Arten werden Anwendungsbereich und Beschränkungen des Zeigerwertsystems aufgezeigt und diskutiert. Das Zeigerwertsystem wird als eine brauchbare Methode betrachtet, um Standorte und Untersuchungsgebiete relativ leicht mit Hilfe der Spinnen zu bewerten. □ *Araneae, indicator value, multivariate analysis.*

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Ecosystems change under anthropogenic influences faster than their structures and functions can be analysed. It is therefore difficult to make well-founded comments about their ability to withstand external pressure, or about possibilities for their protection or renaturalisation. The complex ecological questions this deficit poses will require field work involving as many environmental factors and groups of organisms as possible.

GOALS

A first step is the description of the ecological behaviour of species in the field. A further step is to derive evaluations for the sites, biotopes or areas of study from the ecological behaviour of the species. For example when establishing whether an area should be protected, for purposes of planning and biotope-management as well as when studying the changes at the sites under anthropogenic influence, an efficient evaluation system which beyond that is easy to handle will be necessary.

A number of evaluation systems have recently been developed, e.g. for soil organisms by Wodarz *et al.* (1992), for epigaeic predatory arthropods (spiders and ground beetles) by Haenggi (1987) and Platen (1989, 1992), for spiders by Martin (1991) and for ground beetles by Mossakowski and Paje (1985). Some of these evaluation systems describe the ecological behaviour of the species in the field very precisely (Martin, 1991), or allow a differentiated evaluation of sitse or areas of study (Mossakowski and Paje, 1985; Haenggi, 1987; Platen, 1989). Some evaluation systems, however, have the disadvantage that lengthy calculations are necessary for synoptic evaluation for different sites or areas (Wodarz *et al.*, 1992; Haenggi, 1987). In other cases parameters are used in the calculations which are not stable for time and/or locality, such as a low local abundance of a species, or the numbers of individuals of a species caught in a year (Mossakowski and Paje, 1985). The evaluation systems mentioned can also only be applied locally where, as a result of intensive field work, the ecological behaviour of species along abiotic gradients is known.

A much simpler method would be the applica-

tion of an indicator value system similar to that for plants of Ellenberg *et al.* (1991). It would then no longer be necessary to redetermine and re-evaluate the ecological behaviour of a species for each local investigation, since this would already be contained in the key values. Nor would the evaluation involve complicated calculations.

My aim has been to develop just such an indicator value system for spiders.

MATERIAL AND METHODS

Data

The data consisted of the activity abundances of spider species. These were determined using ground traps in the Berlin area for open and wooded sites in moors, in various types of forest and for heathland and semi-dry and dry meadows. The investigation period was a full year in each case. Activity abundance is defined by Heydemann (1953) as the number of individuals, which has been trespassed a borderline (which is represented by the diameter of the pitfall trap) within a certain period of time. Parallel to the trap catches the following abiotic factors were also measured:

The soil water content (measured as the percentage by volume of water in the upper soil layer), the light exposure using the method described by Friend (1961), and the effective temperature after Pallmannn *et al.* (1940). The sites are described in detail in Platen (1989).

General

The activity abundance of the spider species and the measurements of the abiotic factors are analysed using Canonical Correspondence Analysis (CCA; Jongman *et al.*, 1987), using the program CANOCO Version 3.10 (Braak, 1988, 1991). The results of this analysis are displayed as ordination diagrams using CANODRAW (Smilauer, 1990).

Before running CCA the spider data had been masked according to dominance in a formal way: species which did not have an activity abundance of at least 1% at a site were removed from the data set. This meant that of the original 281 spider species only 111 remained for the further analysis.

Furthermore a transformation of the raw data was carried out. Instead of the abundance values their square roots were used.

RESULTS

Ordination Diagrams

The CCA results with abiotic factors light exposure and temperature, as well as soil water content, are shown graphically (Figs 1, 2). The horizontal axis corresponds to the first CCA axis and the vertical to the second CCA axis. The 111 species of spider are represented by an 'x', together with an abbreviation of the name as far as possible. Using CANOPLOT it was also possible to determine the coordinates and the name of a species which could not be presented unambiguously in the diagram.

Initially the axes of the site factors light exposure and soil water content are extended beyond the origin (Fig. 1). The factor along the 'environmental axes' increases in the direction of the arrow. The origin marks the mean value for the entire data set. Species whose position lies between the arrowhead of an environmental axis and the origin have a larger weighted mean. Where the origin is between the arrowhead and the position of the species, its weighted mean is smaller than the overall mean. For interpretation a perpendicular is projected for each species in turn onto the environmental axis according to their sequence (cf. Jongman *et al.*, 1987). *Xysticus ninnii* and *Thanatus arenarius* occupy the brightest sites, and *Pardosa agrestis* and *Baryphyma pratense* the warmest sites (Fig. 1). Species at extremes of the axes represent limits of the area for a two-factor system, and thus form the start and end points of the indicator value scale. The distance between these points is measured and divided into five equal parts. The species are then noted for each class with the appropriate indicator value.

The determination of indicator values for three factors requires at least two ordination diagrams. Initially an indicator value is assigned for all three individual factors, then for all combinations of two factors. The result always remained the same. For the representation of all three factors in an ordination diagram the class of a species can, however, change, in some cases considerably, since the relative spatial distances of the species in three-factor constellations cannot be represented in a two-dimensional coordinate system without distortion. For the determination of indicator values from the data of individual environmental variables the solution (Figs 1 , 2) is an optimum.

Moisture is strongly negative correlated with the 1st CCA-Axis (Inter-set correlation: -0.919)

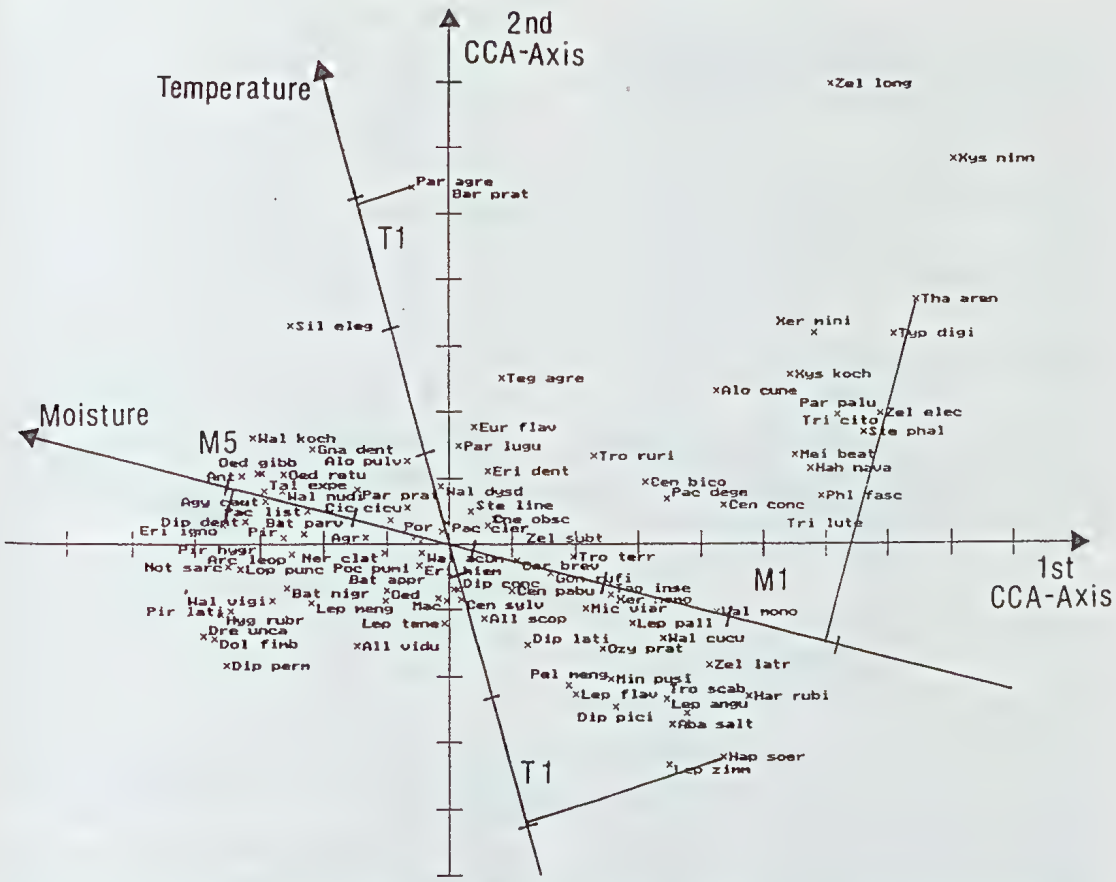

FIG. 1. CCA ordination diagram with 111 spider species represented by an 'x' and environmental variables moisture and temperature represented by arrows. The part of the arrows to derive indicator values are devided into five parts (M1-M5 and T1-T5 respectively). For further explanation see text.

(Fig. 1) which means that the horizontal species distribution is best explained by light and less by temperature (Inter-set correlation with 1st CCA-Axis: 0.26, with 2nd CCA-Axis: 0.538). Hence, the vertical species distribution is best explained along the 2nd CCA-Axis.

The Inter-set correlation between light and 1st CCA-Axis is 0.955 which means that the data set again is best explained by this abiotic factor. Temperature is strongly correlated with 2nd CCA-Axis (Inter-set correlation with 1st CCA-Axis: 0.0367, with 2nd CCA-Axis: 0.6177).

Indicator Values (Table 1)

The last two columns contain details of the ecological type and habitat type in which the species predominantly occurs in the Berlin area (after Platen *et al.*, 1991). The data are intended only to demonstrate the principle of this method. In view of the limited data set the indicator values cannot claim to be comprehensive or generally valid. Some examples will show the similarities and differences between the indicator values and other methods of determining ecological behaviour.

The distribution of *Xysticus ninnii* is centered exclusively on dry meadows. F1, L5, and T4 reflect this ecological behaviour well.

Diplocephalus permixtus: Occurring mostly in wet alder forest-habitats characterised by high soil water content, low light exposure and low temperatures. This is expressed with adequate precision by the indicator values F5, L1 and T2.

Diplocephalus picinus: F2, L1 and T1 characterise its habitat preferences, namely shadowy sites with low pH in dry mixed forests.

Pardosa agrestis: In this case the indicator value does not reflect the ecological behaviour, as a result of the inadequacy of the data set. The species occurs mostly on arable farmland and

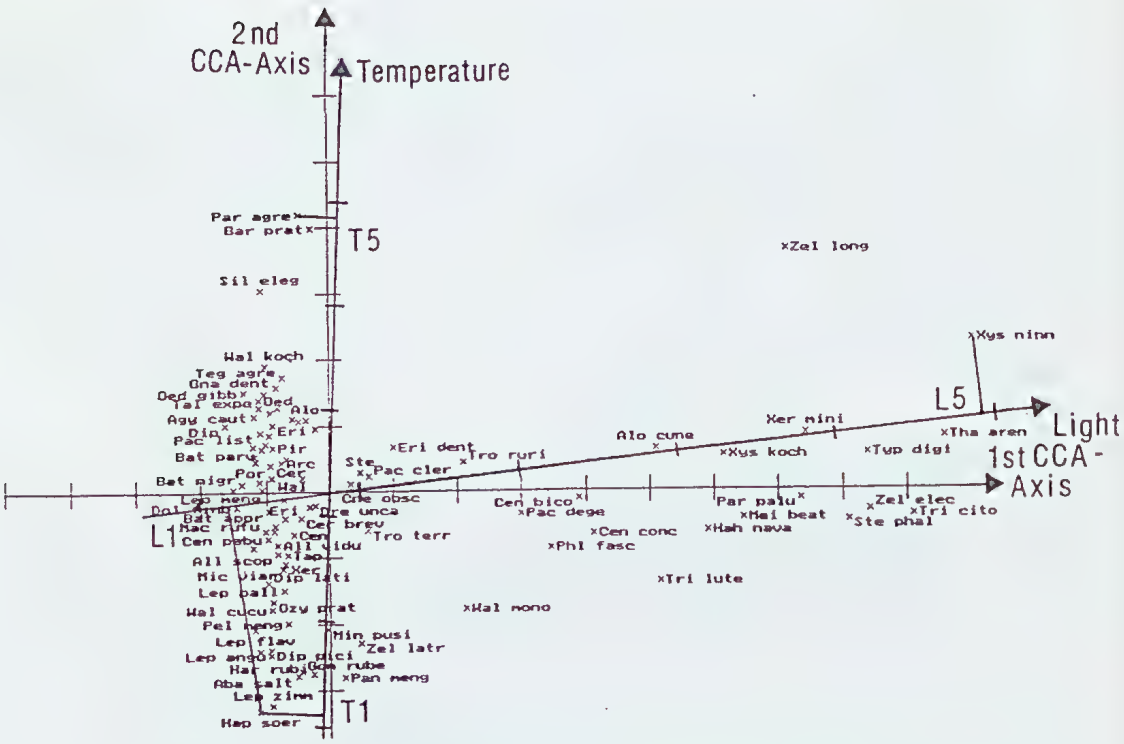

FIG. 2. CCA ordination diagram with 111 spider species represented by an 'x' and environmental variables light and temperature represented by arrows. The part of the arrows to derive indicator values are divided into five parts (L1-L5 and T1-T5 respectively). For further explanation see text.

other open, rather dry habitat types (Platen *et al.*, 1991). While T5 describes the behaviour in terms of temperature, the indicated soil water content (F5) is too high and the light exposure too low (L1). This is because in the data set it only occurred on one site (a former moor which was still wet in comparison to the sites on mineral soils), so that as an outsider it had an extreme position in the ordination diagram. The data set did not include arable farmland sites.

Comments

This method is a relatively easy one to determine indicator values for spiders and other soil arthropods (cf. Platen, 1992).

Indicator values have the advantage that with only a few values the ecological behaviour of a species can be characterised. Mean indicator values can be calculated, and in the absence of the measurements or vegetation surveys they allow a rough quantitative assessment of environmental variables for a investigation site, habitat type or an area of study. The use of indicator values obviates the need for complicated calculations for the evaluation of sites, as required by some evaluation systems (Mossakowski and Paje, 1985; Haenggi, 1987; Platen, 1989).

Some reservations concerning the applications of indicator values are necessary. As already emphasised by Ellenberg *et al.* (1991), indicator values describe the ecological behaviour of species in a multiple system of biotic and abiotic factors, from which those chosen in this paper are regarded as the key abiotic factors for the spiders. They do not, however, describe their physiological optima.

Indicator values for animals underlie more restrictions as those for plants because animals are mobile and often change their habitat for overwintering (Schaefer, 1976). Therefore in the strict sense they are valid only for Adults which does not change their habitat within their period of maturity. As juvenile animals were not included in the data set this holds true for this investigation.

Indicator values should never be used in the same way as measurements. They are ordinal, and are not suited for use in statistical (including multivariate) methods requiring higher scale data.

The indicator values determined above are al-

ways valid only for the data set used. Since they were limited to only a few types of biotope the results above can only be regarded as being a first approximation. The results of the analysis are greatly dependent on the type and number of habitats types and of the frequency with which various species occur there. The combination of a wet, light site (F5, L5) is not represented by an indicator value, although it is relevant for a number of species (*Drepanotylus uncatus*, *Antistea elegans*) (Table 1). However, since almost 2/3 of the 30 sites investigated were wet, and most species occurred with almost the same frequency in wet habitats, these species grouped close to the origin. Species which occur frequently, but only at one or two dry sites with very high light exposure are far from the origin, so that there is a higher differentiation of the axis over the bright range.

A generally valid indicator value system would need to analyse all known spider species of Germany or Central Europe for all existing types of biotope (abiotic factor combinations) in one data set, from which the indicator values could then be derived. The scale could then be expanded, or other environmental factors, such as the biotope structure, could be included. A problem would be the large number of measurements required.

A further problem is that the CCA only depicts species correctly in the ordination diagram if they have an unimodal response curve along a factor gradient (Jongman *et al.*, 1987). By plotting the frequencies of species at all habitat types sorted according to the levels of a factor, it is possible to determine bi-modal, multi-modal or continuous responses. The coordinates of all the habitats where the species occurs with high frequency can be entered in the ordination diagram, making it possible to recognise a corresponding range of occurrence on the environmental axis. For this species, as is the case with some plant species, an indifferent response to this factor for the species or to give a range of the indicator value (cf. Ellenberg *et al.*, 1991) may be possible.

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TABLE 1. Indicator values for soil water content (F), light (L), temperature (T) of 111 common spider species of varying types of habitat. ET=Ecological type: h = hygrophilic, (h) = weakly hygrophilic, x=xerophilic, (x)=weakly xerophilic, eu= euryoecious open-space dwellers, w=forest type, (w) = also in open spaces, hw=sparse forest species, (h)w=inhabits mesophilic deciduous forests, (x)w=inhabits forest on acid soil, h(w)=depending on type of preferred habitat: inhabits unwooded wet habitats or sparse forest. - = no preferred habitats. Family (C): Ag, Agelenidae; Dy, Dysderidae; Gn, Gnaphosidae: Ha, Hahniidae; Li, Linyphiidae; Lc, Liocranidae; Ly, Lycosidae; Ph, Philodromidae; Pi, Pisauridae; Sa, Salticidae; Te, Tetragnathidae; Tr, Theridiidae; Tm, Thomisidae; Zo, Zoridae.

SPECIES	F	L	T	ET	C
Wet Forests					
Pachygnatha listeri Sundevall	5	1	3	hw	Te
Bathyphantes approximatus (O.P.C.)	4	1	3	h(w)	Li
B. nigrinus (Westring)	5	1	3	hw	Li
Diplocephalus permixtus (O.P.C.)	5	1	2	h(w)	Li
Diplostyla concolor (Wider)	4	1	2	(h)(w)	Li
Gonatium rubellum (Blackwall)	3	1	2	hw	Li
Porrhomma pygmaeum (Blackwall)	4	1	3	h(w)	Li
Walckenaeria atrotibialis (O.P.C.)	4	1	2	(w)	Li
Pirata hygrophilus (Thorell)	5	1	3	h(w)	Ly
Deciduous forests					
Centromerus sylvaticus (Blackwall)	4	1	2	(h)w	Li
Ceratinella brevis (Wider)	3	1	2	(h) w	Li
Diplocephalus latifrons (O.P.C.)	3	1	2	(h)w	Li
Gongylidium rufipes (Sundevall)	3	1	2	(h)(w)	Li
Lepthyphantes pallidus (O.P.C.)	2	1	2	(h)(w)	Li
L. tenebricola (Wider)	4	1	2	(h)w	Li
L. zimmermanni Bertkau	2	1	1	(h)w	Li
Microneta viaria (Blackwall)	3	1	2	(h) w	Li
Neriene clathrata (Sundevall)	4	1	3	(h) w	Li
Pardosa lugubris (Walckenaer)	4	1	3	(h) w	Ly
Dry mixed forests					
Harpactea rubicunda (C.L. Koch)	1	1	1	(x)w	Dy
Abacoproeces saltuum (L. Koch)	2	1	1	(x)w	Li
Centromerita concinna (Thorell)	2	3	2	(x)(w)	Li
Centromerus pabulator (O.P.C.)	3	1	2	(x)(w)	Li
Diplocephalus picinus (Blackwall)	2	1	1	(x)w	Li
Gonatium rubens (Blackwall)	2	1	1	(x)w	Li
Lepthyphantes angulipalpis (Westring)	2	1	1	(x)w	Li
Lepthyphantes flavipes (Blackwall)	2	1	1	(x)w	Li
Macrargus rufus (Wider)	4	1	2	(x)w	Li
Minyriolus pusillus (Wider)	2	1	1	(x)w	Li
Panamomops mengei Simon	1	1	1	(x)w	Li
Tapinocyba insecta (L. Koch)	2	1	2	(x)w	Li
Walckenaeria acuminata Blackwall	4	1	3	(x)w	Li

SPECIES	F	L	T	ET	C
W. cucullata (C.L. Koch)	2	1	2	(x)w	Li
W. dysderoides (Wider)	4	1	3	(x)w	Li
W. monoceros (Wider)	2	2	2	(x)w	Li
Euryopis flavomaculata (C.L. Koch)	4	1	4	(x)(w)	Tr
Trochosa terricola Thorell	3	2	2	(x)(w)	Ly
Xerolycosa nemoralis (Westring)	2	1	2	(x)(w)	Ly
Cicurina cicur (Fabricius)	4	1	3	(x)(w)	Ag
Agroeca brunnea (Blackwall)	4	1	3	(w)	Lc
Haplodrassus soerenseni (Strand)	1	1	1	(x) w	Gn
Zelotes subterraneus (C.L. Koch)	3	1	3	(x)(w)	Gn
Ozyptila praticola (C.L. Koch)	2	1	2	(x) w	Tm
Waterside sites					
Gnathonarium dentatum (Wider)	5	1	4	h	Li
Moors					
Agyneta cauta (O.P.C.)	5	1	3	h(w)	Li
Diplocephalus dentatus Tullgren	5	1	3	h(w)	Li
Drepanotylus uncatus (O.P.C.)	5	1	3	h	Li
Erigonella ignobilis (O.P.C.)	5	1	3	h	Li
Lepthyphantes mengei Kulczynski	5	1	3	h(w)	Li
Lophomma punctatum (Blackwall)	5	1	3	h	Li
Notioscopus sarcinatus (O.P.C.)	5	1	3	h	Li
Oedothorax gibbosus (Blackwall)	5	1	4	h	Li
Silometopus elegans (O.P.C.)	5	1	5	h	Li
Tallusia experta (O.P.C.)	5	1	4	(h)	Li
Walckenaeria alticeps Blackwall	5	1	4	h(w)	Li
W. kochi (O.P.C.)	5	1	4	h	Li
W. nudipalpis (Westring)	5	1	4	h	Li
W. vigilax (Blackwall)	5	1	3	h	Li
Arctosa leopardus (Sundevall)	5	1	3	h	Ly
Hygrolycosa rubrofasciata (Ohlert)	5	1	3	h	Ly
Pardosa pullata (Clerck)	5	1	3	h	Ly
P. latitans (Blackwall)	5	1	3	h	Ly
P. piraticus (Clerck)	5	1	3	h	Ly
P. piscatorius (Clerck)	5	1	3	h	Ly
P. tenuitarsis Simon	5	1	4	h	Ly
Trochosa spinipalpis (F.O.P.C.)	5	1	3	h(w)	Ly

TABLE 1. *continued*

SPECIES	F	L	T	ET	C
Dolomedes fimbriatus (Clerck)	5	1	3	h	Pi
Antistea elegans (Blackwall)	5	1	4	h	Ha
Reeds					
Baryphyma pratense (Blackwall)	5	1	5	h	Li
Wet Meadows					
Allomengea scopigera (Grube)	3	1	2	h	Li
A. vidua (L. Koch)	4	1	2	h	Li
Ceratinella brevipes (Westring)	4	1	3	h	Li
Erigonella hiemalis (Blackwall)	4	1	3	(h)(w)	Li
Oedothorax fuscus (Blackwall)	4	1	2	eu	Li
O. retusus (Westring)	5	1	4	eu	Li
Pelecopsis mengei (Simon)	3	1	1	h	Li
Pardosa palustris (Linné)	1	4	3	eu	Ly
P. prativaga (L. Koch)	4	1	3	eu	Ly
Cough-grass sites					
Centromerita bicolor (Blackwall)	2	3	3	(x)(w)	Li
Ruderal sites					
Bathyphantes parvulus (Westring)	5	1	3	eu	Li
Pocadicnemis pumila (Blackwall)	4	1	3	eu	Li
Stemonyphantes lineatus (Linné)	4	2	3	(x)	Li
Trochosa ruricola (De Geer)	3	2	3	eu	Ly
Arable fields					
Bathyphantes gracilis (Blackwall)	4	1	3	eu	Li
Erigone atra (Blackwall)	3	2	3	eu	Li
E. dentipalpis (Wider)	4	2	3	eu	Li
Pardosa agrestis (Westring)	5	1	5	(x)	Ly

SPECIES	F	L	T	ET	C
Tegenaria agrestis (Walckenaer)	4	1	4	(x)	Ag
Heathland					
Tricca lutetiana (Simon)	1	3	2	(x)	Ly
Zelotes latreillei (Simon)	2	1	1	(x)	Gn
Dry grassland					
Pachygnatha degeeri Sundevall	2	2	3	eu	Te
Meioneta beata (O.P.C.)	1	4	3	x	Li
Trichopterna cito (O.P.C.)	1	5	3	x	Li
Troxochrus scabriculus (Westring)	2	1	1	x	Li
Typhochrestus digitatus (O.P.C.)	1	5	3	x	Li
Steatoda phalerata (Panzer)	1	5	3	x	Tr
Alopecosa cuneata (Clerck)	2	3	3	x	Ly
A. pulverulenta (Clerck)	4	1	3	eu	Ly
Xerolycosa miniata (C.L. Koch)	1	4	4	x	Ly
Hahnia nava (Blackwall)	1	4	3	x	Ha
Agroeca proxima (O.P.C.)	4	1	3	(x)	Lc
Zelotes electus (C.L. Koch)	1	5	3	x	Gn
Z. longipes (L. Koch)	2	4	5	x	Gn
Thanatus arenarius L. Koch	1	5	4	x	Ph
Xysticus kochi Thorell	1	4	3	x	Tm
X. ninnii Thorell	1	5	4	x	Tm
Aelurillus v-insignitus (Clerck)	1	5	4	x	Sa
Phlegra fasciata (Hahn)	1	3	2	x	Sa
No obvious habitat preferences					
Cnephalocotes obscurus (Blackwall)	3	1	3	eu	Li
Zora spinimana (Sundevall)	4	1	3	eu	Zo

THE SPIDERS OF THE HIGH-ALTITUDE MEADOWS OF MONT NIMBA (WEST AFRICA): A PRELIMINARY REPORT

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Spiders are abundant in the high-altitude meadows of the Nimba mountains, in Guinea. Collections have been carried out in this ecosystem where grass ground cover is dominant: this preliminary study at the family level concerns specimens collected in March 1991. It already gives some data on the localisation of the spiders. More than 20 families are represented along the mountain tops. A provisional list of these spiders has been drawn up. Most specimens were Araneidae, Gnaphosidae, Hersiliidae, or Salticidae. Their distribution in the herbaceous stratum as well as along an altitude gradient between 800-1700m is being analysed.

Les araignées sont abondantes dans les prairies de haute altitude des Monts Nimba, en Guinée. Des récoltes ont été effectuées dans cet écosystème où la couverture herbacée est dominante. Cette étude préliminaire au niveau des familles concerne les spécimens collectés en mars 1991. Elle apporte déjà quelques éléments sur la localisation des araignées. Plus de 20 familles sont représentées sur ces sommets et une liste provisoire en a été établie. La plupart de ces araignées sont des Araneidae, des Gnaphosidae, des Hersiliidae ou des Salticidae. Leur distribution est analysée dans la strate herbacée ansi que selon un gradient altitudinal entre 800 et 1700m. □*Spiders, biogeography, Africa, montane.*

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The Mont Nimba biosphere reserve, located in West Africa, is the subject of a multidisciplinary study as part of a UNESCO pilot project. These mountains have been classified as an Integral Natural Reserve since 1944. Over the past 50 years, many more animals have been collected during several scientific expeditions directed by Professor Maxime Lamotte (Lamotte, 1943). Many papers have been published on the Nimba mountain range. However works on the spider fauna are non- existent. Hence the organization of the spider populations are still little known. Especially in this tropical region, no work deals with the ecology of spiders except for the research initiatives in the Ivory Coast, in the savanna of Lamto (Lamotte, 1943, 1967; Blandin, 1974; Blandin and Célérier, 1981).

With this subject of research in mind, another field trip was made to Guinea in March 1991. The new collection of spiders made there compliments those of Mr Lamotte and his associates. This abundant material is in the process of being classified. An attempt is being made to describe the structure and function of the spider community in this tropical ecosystem.

The programme focuses on the spiders of the high-altitude meadow, relatively less-frequently collected than those of the savanna or the head of ravines (Lamotte, 1958). This environment is characterized by the strong contrast between the dry and rainy seasons. It presents a characteristic fauna with several endemic species.

In this paper, preliminary data dealing with the localisation of the different families of spiders collected in March 1991 are presented. The overall study will lead to a more detailed inventory of the spiders along the mountain ridges, as well as a better knowledge of their distribution with altitude and the relative abundance of the different species.

ENVIRONMENT AND CLIMATE

Mont Nimba is situated in High Guinea, near the borders of Liberia and the Ivory Coast (Fig. 1). It extends from SW to NE for about 30 km into guinean territory. All the crests stand over 1000m. The mountainside is steep and notched by valleys with sheer slopes. No trees or shrubs are present on the crests. Only some small trees of the inferior savanna grow at lower altitude on the slopes (Schnell, 1966). Above 900-1000m, the forest is confined particularly to the ravines. The mountain range is covered by herbaceous plants with a grassland structure. The term of montane or sub-montane has been given to this

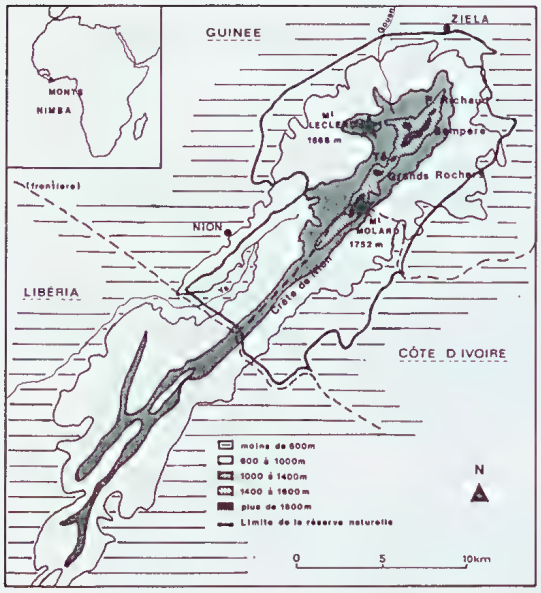

FIG. 1. Map of Mont Nimba, West Africa. Situation of the various sample zones along the Mont Nimba crest.

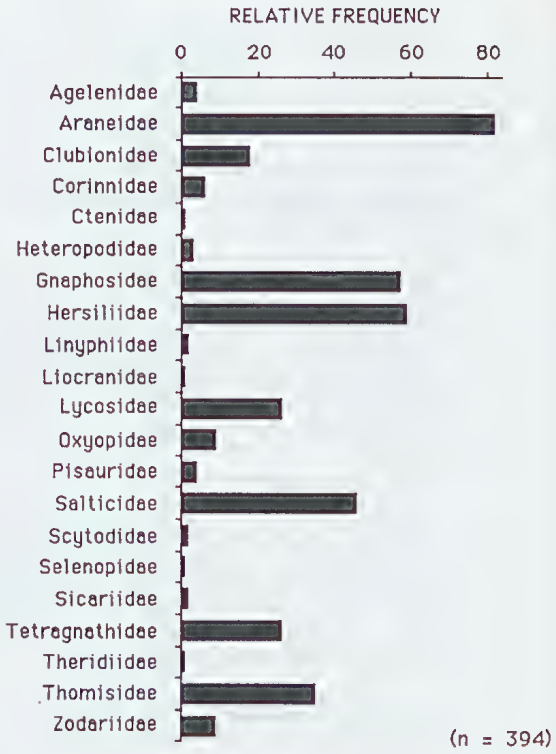

FIG. 2. Total no. spiders taken during March 1991.

crest vegetation (Schnell, 1987). In this type of meadow, located in the guinean part of Nimba, the low (about 20-30cm or less) graminaceous species *Loudetia kagerensis* is abundant and constant. This grass forms a predominant group associated with other tall or short species, varying from site to site.

Mont Nimba receives abundant rainfall and a dry season not exceeding three and a half months. Generally, high-altitude meadows are often covered in fog during the rainy season, from May to November. Precipitation is fine and stable. During the other periods of the year, clouds scale the slopes and progressively cover the crest. Thus the humidity, which is closely bound to the degree of precipitation and nebulosity, varies with altitude and also along the crest. For example, the crest of Nion, spreading upwards to Mont R. Molard in the NE, is wetter than either Mont P. Richaud or the region of Sempéré (Leclerc *et al.*, 1955). Nevertheless, seasonal variations do exist. In the meadow, this factor does not seem to be very important to the ecological cycle of the fauna.

The spiders listed here were collected in March 1991, during the transition period just before the rainy season. Sudden storms or regular strong precipitations occur in the late afternoon from April onwards.

METHODS

Up until now, the high-altitude meadows of Mont Nimba have rarely been sampled. The present study lasted 20 days (8-27 March) with only 14 days of sampling. The first phase consisted in obtaining an overall idea of the spider communities over the whole crest. The collecting program was prepared as follows: 4 days in Sempéré, Grands Rochers; 4 days on the Nion crest, 2 days in Grands Rochers, R. Mollard; 3 days on Mont Leclerc and 1 day in Ziela, P. Richaud.

No strictly quantitative sampling methods were used. Several gathering squares (1m x 1m) were made but the results are insufficient. In addition, these quadrats have not been well materialized because the transport of materials was not easy. Only the sizes were marked by various elements found on the ground. Furthermore, this type of analysis is rare in these environments. Some information on the vertical distribution of the spiders was obtained by the use of beating and ground sweeping methods. A few specimens found on the high sections of the grass were captured, but this is certainly not a representative

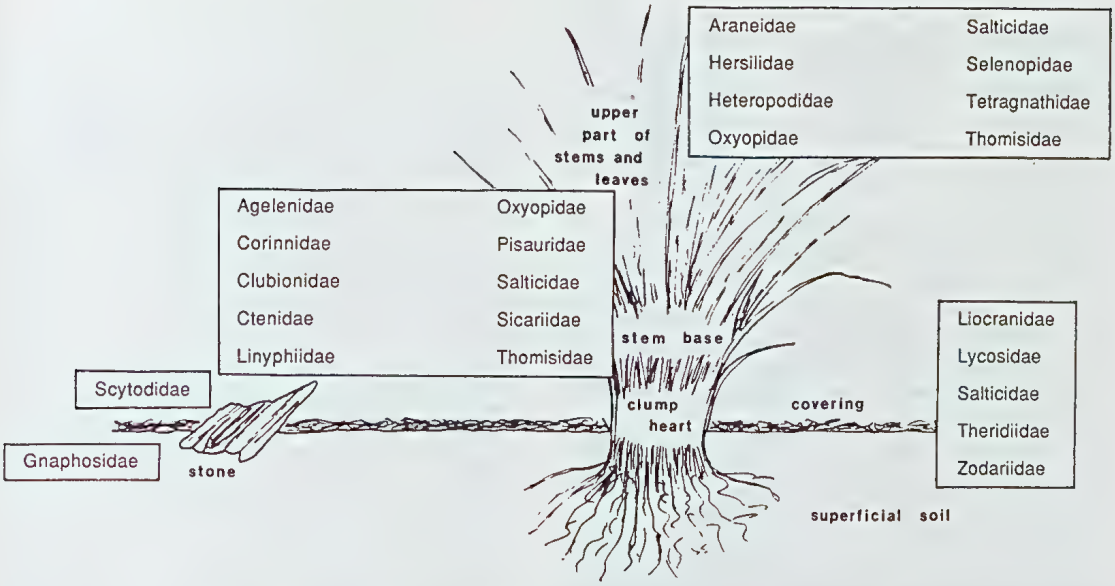

FIG. 3. Distribution of families in epigean environment.

sample of the spider fauna of the herbaceous stratum.

So, in the low herbaceous stratum, samples were made by visual searching in vegetation and under stones, using forceps and pooters. Collecting was only carried out during the daytime and was therefore not exhaustive. The time spent on Mont Nimba was rather short: the researchers stopped collecting at the end of an hour at each site.

A mean of 40 individuals was collected per day, by one to three collectors depending on the days and the availability of the expedition members.

RESULTS

Families Identified

For each sample, the spiders were sorted and enumerated by family. Young and adult spiders were counted together. Immature spiders represent about 54% of all specimens found.

Mygalomorphs were collected, but not in great numbers: 0.5% (2/435). For the moment, the inventory of this suborder has not been established at the family level. Similarly, about 9% (39/435) of the collection is still at the level of indeterminate araneomorph. Therefore, we are only able to present results of the determinate araneomorph families, which correspond to 394 specimens. The names used follow Brignoli (1983) and Platnick (1989).

At least 21 families have been recorded along this crest, of the roughly 100 families known worldwide (Table 1). This relatively high number provides a good idea of the diversity of this environment. The high-altitude meadow-like plateau savanna characterized by the grass species *Loudetia*, is usually considered to be one of the poorest habitats. However, this type of environment clearly possesses an important variety of spiders.

Furthermore, the relative frequencies of these spiders gives another indication of their diversity (Fig. 2). The physionomy of the araneological community is characterized by the predominance of Araneidae which represent around 21% of determined spider families. Four other families were common: Gnaphosidae (57/394), Hersiliidae (59/394), Salticidae (46/394) and Thomisidae (35/394). We note that these spiders are generally large and therefore easier to find. The same observation can be applied to other families which are more easily collected, especially for a certain size. However, the fewer Clubionidae, Lycosidae, Oxyopidae, Pisauridae, Selenopidae and Tetragnathidae in the collections could indicate that they are less abundant in the meadow during this period of the year. The specimens belonging to most other families are generally small and consequently poorly collected. In addition, Liocranidae and Zodariidae are active and move quickly on the soil, so they frequently evaded capture.

Vertical Structure of the Spider Community

The quality of a sampling must take into con-

Agelenidae	Hersiliidae	Scytodidae
Araneidae	Linyphiidae	Selenopidae
Clubionidae	Liocranidae	Sicariidae
Corinnidae	Lycosidae	Tetragnathidae
Ctenidae	Oxyopidae	Theridiidae
Heteropodidae	Pisauridae	Thomisidae
Gnaphosidae	Salticidae	Zodariidae

TABLE 1. List of spider families on Mont Nimba

sideration the biology and the size of the spiders. All families are represented, in spite of the small number of specimens. Around two-thirds of these families frequent the herbaceous stratum and most are diurnal (Fig. 3).

On the upper part of the stems and leaves of plants, the spider community is composed of eight families of which the Araneidae, Tetragnathidae, Hersiliidae and Thomisidae are the most common. The former two build their webs about 20 cm above the soil. Of all Araneidae, Oxyopidae and Salticidae, 25, 2 and 1 specimens respectively were collected by beating and sweeping of the ground. Ten families are present at the base of the stems or in the center of the clumps, Clubionidae being the most abundant. The clubionids are nocturnal hunters and easily found in nests among the vegetation. Five families occur in the superficial soil layer. The Lycosidae constitute most of the collections. Gnaphosidae are mostly nocturnal hunters found in nests among stones. Scytodidae are also found nocturnally active around stones.

Thus, each level of this epigean environment seems to possess its own spider community, characterized by its family composition. Nevertheless, some of them such as the Salticidae, Thomisidae and Oxyopidae are present at all levels of the vegetation and the soil surface. Only analysis at the species level will permit the clarification of the distribution of the spiders in each stratum.

Altitudinal Distribution

The spiders were collected along the crest, mainly situated above an altitude of 1200m. The results are presented by altitudinal classes of 200m, principally because of the small numbers of spiders, and the various sampling zones are indicated in Fig. 1.

An overall view indicates that some families appear to be better represented at the highest altitudes, from 1200m to around 1700m (Table 2). The numbers of Gnaphosidae and Clubionidae regularly increase. Most other families did not

ALTITUDE (m)	800	1000	1200	1400	1600	1800
Oxyopidae	·				9	
Theridiidae					1	
Linyphiidae				2		
Sicariidae				2		
Selenopidae				1		
Ctenidae				1		
Liocranidae				1		
Agelenidae			4			
Corinnidae			6			
Tetragnathidae			26			
Gnaphosidae			5	17	35	
Clubionidae			3	5	10	
Zodariidae		2		7		
Araneidae	4		11	11	56	
Salticidae	4	1	8	9	24	
Hersiliidae	6		22	21	10	
Thomisidae	3	2	9	15	6	
Lycosidae	2	8	8	5	3	
Scytodidae	1				1	
Heteropodidae	2	1				
Pisauridae	3	1				
TOTAL NUMBER OF SPECIMENS	25	15	102	97	155	
NUMBER OF FAMILIES	8	6	10	13	10	

TABLE 2. Altitudinal distribution of spider families in meadow of Mont Nimba.

provide many specimens, with the exception of Tetragnathidae. These spiders are perhaps rare or difficult to observe, but it is all the more interesting to note that their distribution is limited to a certain altitude. In the same way, Eusparassidae and Pisauridae are found only up to 1200m, in low vegetation. The lack of data, between 1000 and 1200m altitude, for the Araneidae and Hersiliidae is probably due to sampling problems. Spiders of these families as well as the Salticidae, Thomisidae and Lycosidae, are certainly present at the different altitudes, and it is likely that the same is the case for the Zodariidae. The family diversity seems to increase slightly with altitude.

The collections made on slopes from 800m upwards concentrated particularly on Mont Leclerc (Table 3). Here too, we note the diversity of the spider fauna, with 14 families present of the 21 listed for Mont Nimba. The same families are found at the highest altitudes. Only Zodariidae and Clubionidae are not encountered below 1400m. Salticidae, Hersiliidae, Thomisidae and Lycosidae can be found from 800 to 1600m.

We also compared the spider families found at three points along the crest: P. Richaud, Grands Rochers and Nion crest, between 1200 to 1600-

	ALTITUDE (m.) 800	1000	1200	1400	1600
Sicariidae				1	
Ctenidae				1	
Liocranidae				1	
Clubionidae				4	
Zodariidae				7	
Gnaphosidae			2	14	
Araneidae	4		3	3	
Salticidae	4	1	2	3	
Hersiliidae	6			12	
Thomisidae	3		3	11	
Lycosidae	2	4	1	3	
Heteropodidae	2	1			
Pisauridae	3	1			
Scytodidae	1				
TOTAL NUMBER OF SPECIMENS	25	7	11	60	
NUMBER OF FAMILIES	8	4	5	11	

TABLE 3. Altitudinal distribution of spider families on Mont Leclerc.

1700m altitude (Table 4). Seven families are present on the Nion crest, clearly a lower diversity than on P. Richaud with eleven families. Six families were observed at all three places. Only Tetragnathidae were found south of the crest. This place seems to be more humid than the others at different periods of the year. The spiders found there are generally hygrophilous species.

For the moment, we cannot provide definitive results on the ecological requirements of the families present only on P. Richaud and Grands Rochers. However, more precise information, at the species level will, hopefully, be available in the future.

COMMENTS

Spiders occupy an important place among the invertebrate fauna of Mont Nimba. They are represented by about twenty families which is a relatively large number for this type of highland meadow. This study is only a first approach; the diversity of the spider community according to stratum and altitudinal level will certainly prove to be rewarding, both quantitatively and qualitatively, with the determination of species. Publication of the final results will probably be delayed because of taxonomic difficulties.

Nevertheless, this study already gives some results at the family level. Prudence in the interpretation of these results is necessary, because the families do not always form homogenous ecological units. The sampling methods used must also be taken into consideration. In the tables and figures, we see that the distributions found are dependent on the collecting effort. In this study we used mostly visual-hunting, with no collecting at night. So we only have a partial sample of the spider families, mainly representing those with diurnal activities. As yet, pitfall traps have not been used to intercept nocturnal spiders. Nevertheless, an estimation of the spiders present along the Mont Nimba crest and their spatial distribution has been made.

We observe several components of this spider

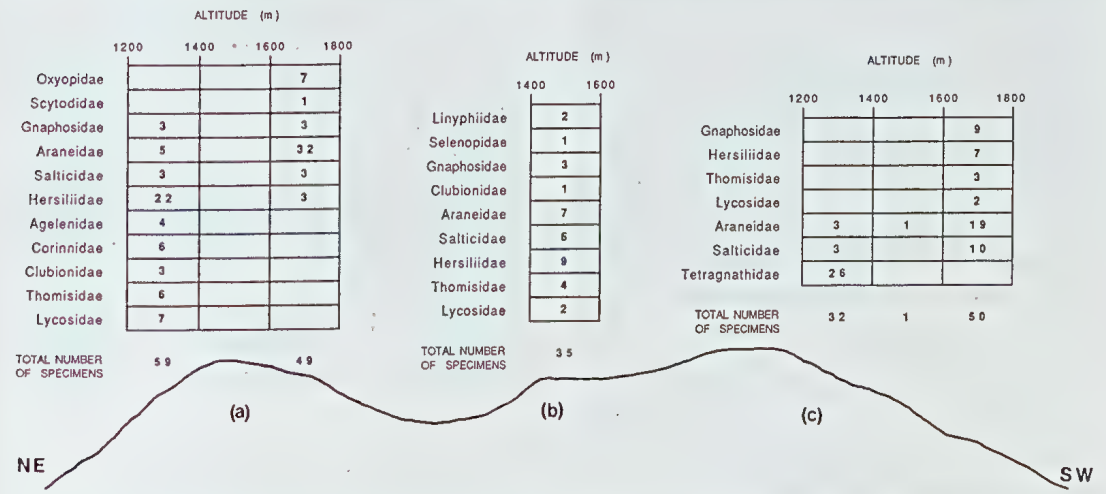

TABLE 4. Altitudinal distribution of spider families along Nimba crest, from SW to NE: (a) Pierré Richaud; (b) Grands Rochers; (c) Nion crest before Richard-Molard.

community, not forgetting the movements of wandering spiders. There are groups on the soil surface principally characterized by Lycosidae and Salticidae; three other families, Liocranidae, Zodariidae and Theridiidae exist in smaller numbers. Groups in the lower part of the vegetation includes ten families, the most with few representatives; Clubionidae, Thomisidae and Salticidae exist in great numbers. A last group exist of the upper part of the herbaceous stratum where Araneidae, Hersiliidae and Tetragnathidae are found in a great numbers; the five other families are less well represented.

The comparison between the northern and southern parts of the crest indicates a possible tendency of one family (Tetragnathidae) to prefer greater humidity. The altitudinal distribution shows that some families, such as Araneidae, Salticidae, Hersiliidae, Thomisidae and Lycosidae, are present from 800 to 1752m. On the contrary, other families are preferentially localised at the highest or lowest altitudes. The spider families found between the altitudes 800 and 1000m, can be considered as being roughly comparable with those present in typical savanna with *Loudetia*. In this environment, there are a great number of spider families (Gillon and Gillon, 1974). More data will be required to confirm these tendencies, as well as their presence on the slopes according to a greater altitudinal gradient and along the whole of the Mont Nimba crest. In addition, some comparisons among sites, including absence of families, might be artefacts, due to relative rareness of representatives.

The study of all spiders collected during the previous expeditions directed by Prof. Lamotte will certainly provide supplementary elements to the various points mentioned in this paper. It will be necessary to characterize, with more precision, the araneological fauna of Mont Nimba. Blandin and Célérier (1981) already noted the misreading of this fauna in West Africa. In addition the well-collected environments are essentially savanna rather than high-altitude meadow.

ACKNOWLEDGEMENTS

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VISUALLY MEDIATED RESPONSES IN THE LYCOSID SPIDER *RABIDOSA RABIDA*: THE ROLES OF DIFFERENT PAIRS OF EYES

J.S. ROVNER

Rovner, J.S. 1993 11 11: Visually mediated responses in the lycosid spider *Rabidosa rabida*: the roles of different pairs of eyes. *Memoirs of the Queensland Museum* **33**(2):635-638. Brisbane. ISSN 0079-8835.

Video images of conspecifics were presented to *Rabidosa rabida* (Walckenaer) (Araneae: Lycosidae) to study the roles of different pairs of eyes in a wolf spider. Four groups of spiders had one pair of eyes occluded, and four had all but one pair occluded. Various control groups were also tested. The PLE were essential for sizeable orientation turns of up to about 160°. The PME served for rapid, long distance approaches toward the stimulus; they also initiated orientation turns of up to about 50°. If close to the stimulus, the ALE initiated small turns of up to about 20° and mediated small approaches. The AME did not mediate any responses. Courtship could be triggered in males via the PLE or the PME. In females, only the PME mediated receptive display responses to temporally patterned leg I movements seen in anterior or lateral views of a courting male. □*Araneae, Lycosidae, eyes, vision, communication.*

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Very little behavioural research has been carried out on vision in lycosid spiders, compared to the extensive studies on salticid spiders (reviewed in Forster, 1985). In lycosid spiders, occlusion of the eyes has been used to test for differences in the roles of the main vs. secondary eyes (Homann, 1931) as well as the anterior vs. posterior eyes (Acosta *et al.*, 1982); however, the results of both of these studies were confounded by the lack of controls for vibratory stimuli. The only successful behavioural investigation of the role of particular eyes in lycosids (Magni *et al.*, 1964) demonstrated the importance of the AME in astronomical orientation and was accomplished by covering all but a single pair of eyes in each group tested. Occlusion of only one pair of eyes at a time has proven useful in several behavioural studies of salticid vision (e.g., Forster, 1979).

In the present study of the lycosid spider *Rabidosa rabida* (Walckenaer), I used both methods of occlusion to examine the roles of different pairs of eyes in detecting visual stimuli and mediating appropriate responses. By using video images as stimuli (Clark and Uetz, 1990), I eliminated the possibility that vibrations or chemicals from conspecifics could confound the results.

METHODS AND MATERIALS

Penultimate *Rabidosa rabida* (formerly *Lycosa rabida*) were collected in late June (1990 and 1991) in Athens County, Ohio, USA. The methods of maintenance and the laboratory conditions during testing have been described previously (Rovner, 1989). Spiders were not used in testing until 1 week after the final moult. Tests were conducted between 1000 and 2200 hours.

For each test the spider's home cage, with its resident within, was placed with its narrow front side facing a small television set (black and white Magnavox BH-3907; screen = 9.2cm wide, 6.6cm high), which received a playback signal from a Sony recorder (SL-HFR70). The clear front side of the plastic cage (the other sides were opaque) was 7cm wide and was located 3cm from the screen. I removed the cage cover and, if necessary, gently positioned the spider with an artist brush to insure that the screen would be within the visual field of the spider's useable eyes. (I used separate brushes for males and females). Then, a glass cover (one for each sex) was placed on top of the cage. A front-silvered mirror fixed at 45° to the floor was 0.5m above the cage. A video camera (JVC GX-8NU) was aimed at both the mirror and an adjacent, second, identical television set receiving the same signal from the playback recorder as the first set. This yielded (on a second, identical recorder) a kind of split-screen recording. On the left was a dorsal view of the spider, which facilitated the measurement of turning angles (accurate to the nearest 5°) and speeds of locomotion. On the right was a view of the video image concurrently being presented to the spider. Thus, the relationship of

the video stimulus to the spider's response could later be analyzed.

Subjects used for video presentations were recorded against a plain, pale background and illuminated evenly by a 32-W, circular fluorescent bulb 0.5m above the arena. The camera was located at a distance yielding a screen image the size of the actual subject (average body lengths: female=18mm; male=12mm). The 15-min video playback for females was a pheromone-stimulated, courting male; his occasional position changes provided nearly equal proportions of anterior and lateral views of his display (total number of courtship bouts = 51). The 10-min video playback for males was a lateral view of a female walking to and fro in an elongate glass arena (passes across the screen =15 leftward and 15 rightward). Some preliminary tests made use of prey images provided by a 10-min video of three crickets (*Acheta domesticus*, 10mm body length) walking to and fro.

To cover the eyes of spiders, I painted them with two coats of water-based enamel (Top Color Hobbylack, Pelikan AG). That this insured complete occlusion had been established previously (Rovner, 1989). Spiders were tested one or more days later.

I ran two preliminary tests to see if painting or its related procedures lowered responsiveness. All the eyes of five females were covered with two separately applied coats of clear paint. Five other females were briefly anaesthetised (carbon dioxide) and then restrained for 6 hr, thereby duplicating the procedure used when painting the eyes. However, at the two times that paint would have been applied (0 hr and +3 hr), I used water instead. The next day, when exposed to video images of crickets, the clear-painted spiders were less responsive than were the water-brushed spiders. The latter seemed as responsive as untreated spiders.

There were three control groups, each with 10 females and 10 males; these 60 individuals were given two trials apiece. One group consisted of untreated spiders exposed to the conspecific video playback, to determine how readily fully sighted spiders respond. A second group, also untreated, was exposed to a 10-min video of an empty arena, to determine if that alone had a stimulating effect. (Light from the screen = about 800 lux; incident light from above = about 350 lux.). The third group consisted of fully blinded spiders exposed to the conspecific playback, to see if such spiders would perform behaviours (orientation, rapid approach, or display) that I assumed would only occur in this study as visual responses.

There were eight experimental groups, each having 10 spiders of each sex. In four experimental groups a single pair of eyes was occluded; in four others, all but one pair was occluded. Since one of the untreated control spiders had failed to respond to video playback within two trials and since the preliminary tests had indicated that painting the eyes can reduce responsiveness, I gave unresponsive experimental spiders additional opportunities to respond, up to a limit of five trials. One or more days separated consecutive trials undergone by any individual spider.

RESULTS

During testing of control groups, all of the untreated females and all but one of the untreated males showed 'orientation' and/or 'long-range approach.' Most (16/20) did so in the first trial. 'Orientation' involved a single, rapid pivot that resulted in the spider facing the image. This pivot had a mean speed (SD) of 121 ± 51.7°/s ($N = 12$), about eight times faster than turns that occurred during wandering, 16 ± 12.4°/s ($N = 11$). A 'long-range approach' covered a distance of up to 10cm, the maximum being limited by cage depth (12.5cm). The speed of an approach, 5.9 ± 3.32 cm/s ($N = 22$), was about ten times faster than walking during wandering, 0.6 ± 0.31cm/s ($N = 36$). (The above speeds are not the maxima attained, since I included the acceleration and deceleration phases in each bout of locomotion.) No orientation or approach responses occurred in the empty arena or fully blind controls.

Results of the eye occlusion experiments are summarized in Table 1. Spiders with any one of the four pairs of eyes occluded were still capable of orientation; those with occluded PME did not show approach. When all but one pair of eyes was occluded, the only group failing to show orientation was the one limited to use of the AME; and the only group that still showed long-range approach was the one with useable PME. When close to the cage front, a few spiders having only useable ALE did perform a near-field approach response, edging forward less than one body length. For all the responding experimental groups, the mean number of trials (± SD) needed to obtain either an orientation or a long-range approach to the image was 1.2 ± 0.53 ($N = 63$) for females and 2.4 ± 1.24 ($N = 55$) for males (Mann-Whitney *U*-test, $Z = -6.545$, $P < 0.0001$).

Spiders with useable PLE showed orientation

Condition	Orientation		Long range approach		Display	
	♀	♂	♀	♂	♀	♂
Untreated	6	6	8	7	3	5
Empty arena	0	0	0	0	0	0
Fully blind	0	0	0	0	0	0
No PLEs	6	7	10	4	5	3
No PMEs	10	6	0	0	0	4
No ALEs	10	7	9	5	4	4
No AMEs	10	6	9	6	4	3
Only PLEs	10	7	0	0	0	5
Only PMEs	9	6	10	5	5	2
Only ALEs	3	1	0	0	0	0
Only AMEs	0	0	0	0	0	0

TABLE 1. Number of ♀ and ♂ spiders responding to video playback. $N = 10$ spiders/sex/condition. Each spider was allowed more than one trial to respond: controls, up to two trials; experimentals, up to five trials. Only ♂♂ that also performed orientation or approach are included under 'Display'.

turns of up to about 160°. Those with only the PME useable performed orientation turns of up to about 50°. If near the stimulus, those with only the ALE useable showed orientation turns of up to about 20°.

During playback of male courtship, only those females with non-occluded PME performed leg-waving receptive displays (Table 1). This brief display occurred 3.0 ± 1.9s ($N = 30$) after the abrupt termination of the male's courtship bout. The receptive display was sometimes performed unimpeded, this being the case in females which had not yet reached the front of the cage. However, it was usually constrained, since most females quickly approached the cage front and rested their anterior legs against the wall. Still, the timing of their response remained precise. Females showed this display while seeing anterior or lateral views of the courting male.

Up to 6/10 of the males tested in each condition performed courtship display, which occurred in every group. It even occurred in two males during the empty arena playback and in three of the fully blinded males, such data reflecting a previously noted readiness of *R. rabida* to sometimes court in response to subnormal stimuli (Rovner, 1968). Perhaps these non-visually stimulated courtships were triggered by mechanical cues resulting from my moving the cage to the testing site or from my positioning the spider with a brush (to duplicate the procedure used on experimental spiders). For this reason, only courtships occurring during trials in which orientation or approach also occurred were scored as visually initiated displays. (This may have prevented some visually stimulated males that were facing the stimulus at the outset from being included in the courtship total for some experimental groups.) Only males with useable PLE or PME showed courtship accompanied by orientation, and only males with non-occluded PME showed courtship accompanied by approach (Table 1).

DISCUSSION

Data presented here indicate that *R. rabida*'s posterior eyes play major roles in mediating responses to important visual stimuli, as was earlier predicted for lycosids on anatomical grounds (Homann, 1931; Land, 1981). The PLE serve the same function that they do in salticid spiders, that of detecting stimuli in an extensive visual field and initiating the largest orientation turns. They cannot mediate approach behaviour. On the other hand, the PME are essential for mediating rapid, long-range approaches to stimuli. They can also initiate orientation turns of up to 50°.

As to the anterior eyes, at close range the ALE can play small roles in orientation and approach. This contradicts Land's (1981) suggestion that only the large posterior eyes are involved in prey capture. As predicted for lycosids by Land (*ibid.*), the AME of *R. rabida* play no role by themselves in mediating turns or approaches toward a target. Whether they serve for other than polarized light detection (Magni *et al.*, 1964) remains to be explored.

The present findings on the anterior eyes of *R. rabida* may not apply to all lycosids. For example, unlike *R. rabida*, in *Arctosa variana* the AME are larger than the ALE (*ibid.*). Also, local tiering is found in the retinae of the AME of *Geolycosa godeffroyi* but not in the type genus *Lycosa* (Blest and O'Carroll, 1989). Furthermore, the finding of high nocturnal sensitivity in the anterior eyes of *Lycosa tarentula* (Carricaburu *et al.*, 1990) suggests that an understanding of the capabilities of the anterior eyes of lycosids will require examining different species under various illumination conditions. Finally, I must point out that I did not test for any possible collaboration between different pairs of eyes. Collaborative visual mechanisms were revealed in salticid spiders by ipsilateral blinding (Forster, 1979).

As in the salticids (Forster, 1985), orientation and approach are the initial behavioural responses of lycosid spiders to moving images, whether prey or mating partners. Thus, the performance of such behaviours does not specify the spider's

motivational state. However, the fact that twice as many trials were needed to obtain these behaviours in males as in females suggests that such initial responses relate primarily to predation, i.e., that adult females, on average being hungrier than males, are more responsive to visual stimulation. A subsequent occurrence of display behaviour indicates a switch to sexual motivation.

For display to occur in females the PME have to be useable, and they are sufficient by themselves for mediating this response. The fact that lateral as well as anterior views of the courting male elicited responses suggests that the cue is movement of the male's black leg I: it extends forward in a pumping-like motion of increasing frequency and then abruptly flexes back. Unlike salticid face-to-face courtship, in which the perceived form of the male may be as important for the female as his behaviour (*ibid.*), female *R. rabida* need not view the male's anterior. Apparently, detection of a temporal pattern of movement suffices for recognition.

As to visually-triggered courtship display, male *R. rabida* differ from male salticids, which require one particular pair of eyes, the AME (*ibid.*). Stimulation of either pair of a male *R. rabida*'s posterior eyes suffices for triggering courtship. If the PLE are involved, orientation precedes display. If the PME are involved, approach can precede display, although it need not do so.

Given that the movement-detecting PLE are sufficient for courtship onset in *R. rabida*, an adequate stimulus in this species may be any object of an appropriate size, speed, and perhaps movement pattern entering the extensive visual field of the PLE. Since the other three pairs of lycosid eyes are also assumed to be movement detectors (Land, 1981), there may be no need to require their involvement in additional visual analysis before initiating courtship. However, this may not be true for all lycosids. In particular, female *Pardosa laura* have been hypothesized to use form vision for species discrimination (Suwa, 1984). If male *P. laura* likewise do so, eyes other than the PLE would be have to be used for such form analysis in order to inititate courtship.

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THE SPATIAL DYNAMICS OF LINYPHIID SPIDERS IN WINTER WHEAT

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The density of linyphiid spiders was monitored accurately throughout the growing season in a field of winter wheat in southeast England in 1990 and 1991. Numbers increased until harvest in 1991, but declined before harvest in 1990, possibly due to drought conditions. The pattern of natality in 1991 closely mirrored the pattern of change in density, suggesting that reproduction, rather than immigration, was the predominant factor underlying the increase in density. Aerial activity, as measured by deposition traps and a rotary trap in the field, and a suction trap at the edge of the field, increased progressively during the growing season. Results from a short-term field caging technique, used to measure net migration rates, indicated that there was little immigration before July (thereafter high sampling variance, caused by aggregation in weedy patches, precluded meaningful analysis).□*Araneae, Linyphiidae, spatial dynamics, winter wheat, density, natality, migration.*

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There are few studies of the population dynamics of predators. For example, Stiling (1988), in an examination of the incidence of density-dependence in invertebrate populations, quotes 62 population dynamics studies; of these 60 relate to phytophages, 2 to parasitoids and none to predators. There are also few population dynamics studies of migratory species, because of the methodological problems involved in quantifying migration. The present study, of the population dynamics of linyphiid spiders (the species concerned are all migratory predators), was undertaken to collect some basic data in this neglected area, and also because these species are known to be valuable predators of crop pests (Sunderland *et al.*, 1986). This paper summarises the main trends for total linyphiids; consideration will be given to individual linyphiid species in later publications.

METHODS AND MATERIALS

Total spider density was measured throughout most of the growing season of 1990 in a 17ha field of winter wheat (c.v. Pastiche) in southeast England. In 1991, density, natality and migration were measured in a 3ha field of winter wheat (c.v. Riband), 24km from the 1990 study field. The fields were treated with agrochemical applications, following normal farm practice; insecticides were not required in either year.

Density Sampling

Twenty-five 144m^2 squares were marked out inside a 60 x 60m area (adjacent to one edge of the field in 1990 and 30m from the nearest edge in 1991). Fifteen density samples were taken at each sampling interval (approximately weekly) following a Latin Square design. The sample unit consisted of a randomly-selected 0.5m^2 area of ground delimited by a metal ring and sampled using a vacuum insect net (D-vac). Vegetation and the top 1cm of ground, within the 0.5m^2 sampled by D-vac, were then immediately hand-searched for spiders. The suction catch was kept at 10°C and returned to the laboratory for live-sorting. Therefore spiders were collected from 7.5m^2 of habitat (crop, ground surface and immediate sub-surface) on each occasion (Topping and Sunderland, 1992). The D-vac collected only about 50% of the total number of spiders present in a sample unit, the other 50% were uncovered by hand-searching (see also Sunderland *et al.*, 1987).

Natality

Adult female linyphiids were collected from the field, adjacent to the 60 x 60m area, at weekly intervals and incarcerated individually in 9cm diameter plastic Petri dishes lined with moist filter paper. The dishes were returned immediately to a ventilated box in the study field and examined at weekly intervals. Mean daily temperatures in the Petri dishes did not diverge from field temperatures (measured on the ground

surface, under weed cover) by more than 1°C (warmer in spring, cooler in summer). The dishes were inspected at weekly intervals and the following statistics recorded (i) proportion of spiders producing eggsacs in the first week of incarceration, (ii) time (days) to emergence of spiderlings, (iii) number of spiderlings emerging, and (iv) number of undeveloped eggs (by dissection of the eggsac). These results were used, in conjunction with information on the density of adult females, to calculate daily natality rates for each species and then combined to give a composite spider natality curve.

Net Migration Rate

Migration to and from small areas of the crop was suppressed by the use of ten stainless steel spider-proof cages. The cages were circular, $0.5m^2$ by 1m tall, and made of mesh with 3 x 2.5 perforations mm^{-2} (too small to allow passage of first instar linyphiid spiders). The bases of the cages were sealed with sufficient compacted soil to prevent entry or exit of any spiders. Total spider density inside the cages was assessed as above. Because the cages were moved to a new location within the Latin Square each week, there was assumed to be insufficient time for the processes of natality and mortality to be significantly affected by the changed microclimate inside the cages; therefore differences in the change in density from one week to the next between caged and uncaged parts of the crop were considered to be a measure of net migration.

Aerial Density of Spiders

A 46cm Propeller Suction Trap (Taylor, 1955), with an air throughput of $70m^3$ min^{-1} and a sampling height of 142cm above the ground surface, located at the edge of the study field, was emptied daily. In addition, a rotary insect net was used to collect spiders within the field, 25cm above the top of the crop canopy. The 10m long rotor arm travelled at 6.3m sec^{-1} and the 56 x 25cm net at the end of the rotor arm (which was designed to sample air isokinetically, (Taylor, 1962)) processed $53.8m^3$ min^{-1} and was also emptied daily. To measure rates of input of spiders into the field, a set of seven deposition traps were deployed at 15m intervals between the rotor and the 60 x 60m area. Each trap consisted of a 10cm deep, $1m^2$, fibreglass tray, filled with water and ethylene glycol (20:1) plus 1% detergent, fitting inside a $1.6m^2$ metal tray containing the same fluid. The outer tray acted as a barrier to prevent spiders walking from the crop into the inner tray, which therefore received only aerial immigrants. As the crop grew, the deposition traps were progressively raised on wooden supports to maintain the level of the fluid surface constantly at *ca.* 5cm above the top of the crop canopy. The traps were emptied at approximately weekly intervals.

Nomenclature follows Roberts (1987).

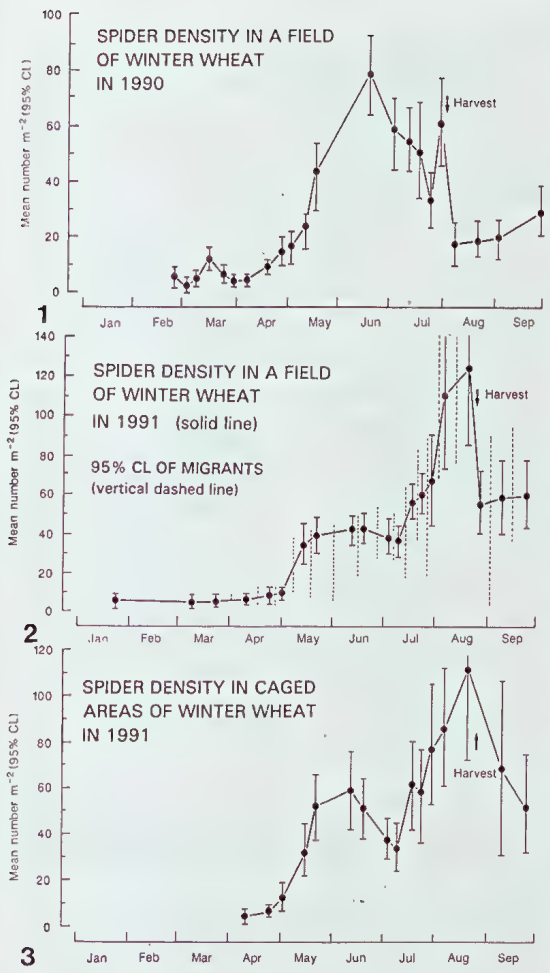
RESULTS

The study was based on data from more than 39,000 individuals belonging to 53 species. 12 species were dominant (Table 1). All species belong to the family Linyphiidae, with the exception of the tetragnathid *Pachygnatha degeeri*. *Lepthyphantes tenuis* was the most abundant species in 1991 and the second most abundant in 1990. Species composition was similar in the two years, the only notable differences being that *Meioneta rurestris* was relatively more abundant in 1990, the reverse being true for *Oedothorax* spp. Here, all spiders are treated as a group.

In 1990, density of total spiders increased in spring to reach a peak of $78m^{-2}$ on 18 June and thereafter declined, apart from a short-lasting peak (made up entirely of immature spiders) just before harvest (Fig. 1). The pattern was different in 1991 (Fig. 2); spider density built up in two steps (the first in May/June, the second in August) to reach a peak of $123m^{-2}$ just before harvest. Mean air temperatures in June and July were slightly higher in 1990 (15.1°C) than 1991 (14.9°C), but rainfall was considerably lower (68mm in 1990 cf 191mm in 1991). The semi-drought conditions in the summer of 1990 may have had a deleterious effect on spider survival.

Species	1990	1991
Meioneta rurestris (C.L. Koch)	32.5	5.4
Lepthyphantes tenuis (Blackwall)	27.8	31.3
Erigone atra (Blackwall)	9.8	13.3
Milleriana inerrans (O.P.-Cambridge)	5.2	0.4
Erigone promiscua (O.P.-Cambridge)	5.0	6.3
Erigone dentipalpis (Wider)	4.2	5.0
Pachygnatha degeeri Sundevall	2.0	0.2
Bathyphantes gracilis (Blackwall)	2.7	8.6
Oedothorax fuscus (Blackwall)	2.4	12.0
Oedothorax retusus (Westring)	2.1	3.9
Panamomops sulcifrons (Wider)	1.0	0.1
Oedothorax apicatus (Blackwall)	0.3	6.9
Others*	5.0	6.6

TABLE 1. Species composition of adult spiders in density samples in 1990 (n=1562) and 1991 (n= 1457).



FIGS. 1-3. Total spider density in a field of winter wheat: 1990 (Fig. 1); 1991 (solid line) and 95% CL of number of migrants m^{-2} (vertical dashed lines) (Fig. 2); in caged areas, 1991 (Fig. 3).

Density in the caged areas of the crop in 1991 followed a similar pattern to that in uncaged areas (Fig. 3). 95% confidence limits increased during July and August (Figs 2, 3) due to aggregation of spiders in weedy patches of the crop (significantly more spiders in weedy than bare areas; paired t-test, n = 5 dates, p = 0.05).

The pattern of change in density with respect to time is examined, below, in relation to natality and migration for 1991.

Natality rates were *c.* $4m^{-2}$ day^{-1} in the spring, briefly 10-$15m^{-2}$ day^{-1} in late July, then $8m^{-2}$ day^{-1} in August. The pattern of daily natality was similar to the patterns for immature spider density (Fig. 4) and total spider density (Fig. 2); this is

Date	M	95% CL
9 April	2.1	(-1.2- 5.4)
23 April	2.2	(-2.3- 6.7)
1 May	-2.0	(-8.7- 4.7)
14 May	2.7	(-11.8-17.2)
21 May	-12.8	(-29.5- 3.9)
11 June	-16.5	(-33.9- 0.9)
18 June	-8.0	(-23.1- 7.1)
3 July	0.7	(-13.2-14.6)
9 July	2.9	(-10.4-16.2)
17 July	-5.1	(-26.7-16.5)
23 July	1.8	(-20.5-24.1)
29 July	-9.5	(-43.8-24.8)
5 August	24.2	(-19.9-68.3)
19 August	12.7	(-41.4-66.8)
9 September	-10.0	(-52.7-32.7)
24 September	7.1	(-19.6-33.8)

TABLE 2. Indices of net aerial migration, M (95% CL), in 1991.

circumstantial evidence that reproduction (as opposed to immigration) is the predominant process driving increase in density of spiders in the field. Data on migration can be examined in the light of this hypothesis. Aerial activity of spiders, as measured by catches in the 1.4m suction trap at the edge of the field, tended to increase steadily from March to August, and this was followed by a much larger increase in September (Fig. 5). A similar pattern of aerial activity was evident inside the field, as indicated by the catch in deposition traps and in the rotary trap (Fig. 6). To assess whether there had been a a net gain or loss of spiders from the field over a particular period, the density of spiders inside caged areas was compared with the density outside,to give an index of net migration (M);

$$M = (F2-F1)-(C2-F1) = F2-C2$$

where F1 and F2 are densities in the uncaged part of the field in weeks 1 and 2 respectively, and C2 is the density in the caged part of the field in week 2. (F2-F1 represents change in numbers due to natality, mortality and migration, whereas C2-F1 represents change in numbers due to natality and mortality alone, because migration was suppressed by caging). The standard error of M is calculated as the square root of [$SE\ F2^2$ + $SE\ C2^2$]; the 95% CL's on M are therefore large because they are compounded of two standard errors. Values of M are shown in Table 2. Positive values indicate immigration and negative values indicate emigration. However, all 95% CL's span the range from negative to positive and therefore no significant net migration can be demonstrated.

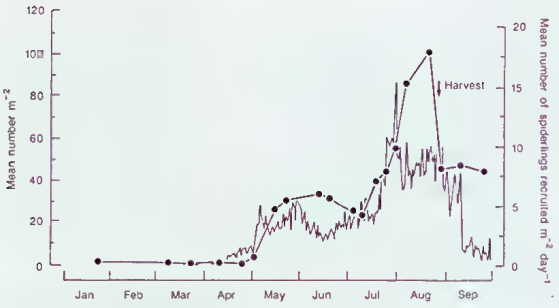
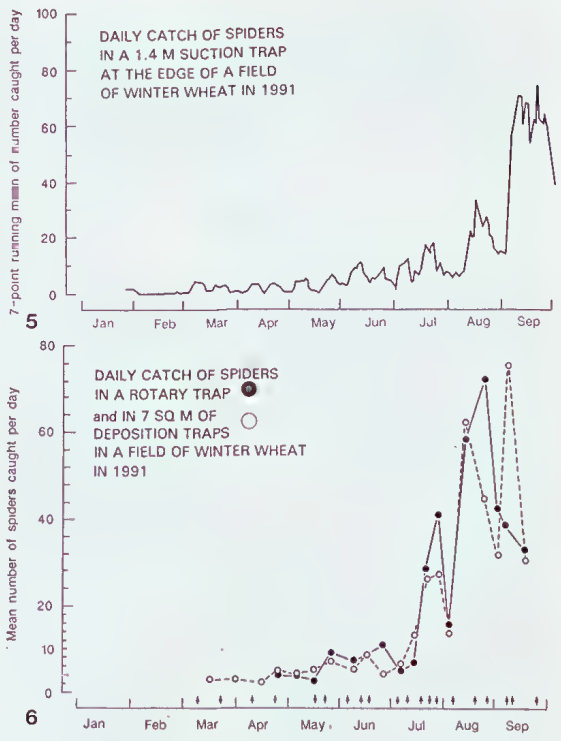


FIG. 4. Total immature spider density (●) and total spider natality (continuous line) in a field of winter wheat in 1991.



FIGS. 5, 6. Daily catch of total spiders in winter wheat field in 1991. 5. In 1.4m suction trap at edge of field; 6. In rotary trap (●) and in $7m^2$ of deposition traps .

These 95% CL's are plotted on the curve of total spider density (Fig. 2); the extent of the dotted line above and below the density curve shows the amount of immigration and emigration, respectively, that could have occurred between any two dates. The following conclusions can be drawn; (i) any migration that may have occurred in April was small (i.e. on a similar scale to density sampling variance), (ii) if immigration occurred in May and June it must also have been on a small scale, but there could have been a large emigration, and (iii) in July, August and September 95% CL's were very large (due to spider aggregation, see above), with no obvious bias in favour of either immigration or emigration.

DISCUSSION

There appear to be no previous quantitative arachnological studies in which the seasonal patterns of natality and migration are compared with the seasonal pattern of density using consistent units. Examples of other arachnological studies involving density or natality estimation are given below. The majority of investigations where density has been measured are for grassland; peak densities of lycosid and linyphiid spiders vary greatly according to location (Table 3). Densities are often lower in graminaceous crops (Table 3). The peak spider density of $123m^{-2}$ in the present study is comparable with, if somewhat greater than, densities recorded in cereals by other authors (Table 3). In common with the present investigation, nearly all the studies in Table 3 reported large confidence limits due to aggrega-

Species	Family	Habitat	Density	Author(s)
Geolycosa godeffroyi (L.Koch)	Lycosidae	pasture	1	Humphreys, 1976
Trochosa terricola Thorell	Lycosidae	grass heath	70	Workman, 1978
Pardosa palustris (Linnaeus)	Lycosidae	alpine meadow	9	Steigen, 1975
Oedothorax fuscus (Blackwall)	Linyphiidae	pasture	155	De Keer and Maelfait, 1987
Erigone atra (Blackwall)	Linyphiidae	pasture	318	De Keer and Maelfait, 1988
Erigone arctica (White)	Linyphiidae	dune grass	330	van Wingerden, 1977
Total spiders		*Festuca* grass	840	Duffey, 1962
Total spiders		rye grass	43	Alderwiereldt, 1987
Total spiders		maize	49	Alderwiereldt, 1987
Oedothorax and *Erigone*	Linyphiidae	winter wheat	53	Nyffeler and Benz, 1988
Total linyphiids		winter wheat	60	Fraser, 1982
Total spiders		winter wheat	75	Sunderland 1987

TABLE 3. Maximum density estimates (number m^{-2}) in a range of arachnological studies.

tion of spiders. There seem to be no previous publications describing the seasonal pattern of spider natality, but a few authors (eg Steigen, 1975; Workman, 1978) have recorded natality at specific times of year. Schaefer (1978) estimated the egg density of the linyphiid *Floronia bucculenta* in grassland during the spring to be 98-151m^{-2} depending on location. The maximum spring natality of the linyphiid *Erigone arctica* in coastal grassland was claimed to be 2584m^{-2} (van Wingerden, 1977), which is considerably greater than the total natality (8 dominant linyphiids) of 789m^{-2} between March and October in the present study; this difference may underly the relative sparseness of spiders in crops compared with natural grassland (Table 3). Although the intensity of aeronautic activity has been measured using sticky traps (Duffey, 1956, van Wingerden, 1977, Greenstone *et al.*, 1985), window traps (Meijer, 1976; De Keer and Maelfait, 1987, 1988) and suction traps (Dean and Sterling, 1985; Sunderland, 1987, 1991), there appear to be no previous attempts to directly quantify the impact of migration on population density. The use of short-term field cages in the present study provided useful estimates of the upper limits to migration (except when sampling variance became very large) and it is expected that this technique will yield better results when data are analysed for individual species. In addition, when the rotary trap has been calibrated, it should be possible to estimate rates of aerial immigration and emigration from a comparison of deposition and rotor catches.

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MORPHOLOGY OF THE EMBRYOS AT GERM DISK STAGE IN *ACHAEARANEA JAPONICA* (THERIDIIDAE) AND *NEOSCONA NAUTICA* (ARANEIDAE)

HIROHUMI SUZUKI AND AKIO KONDO

Suzuki, H. and Kondo, A. 1993 11 11: Morphology of the embryos at germ disk stage in *Achaearanea japonica* (Theridiidae) and *Neoscona nautica* (Araneidae). *Memoirs of the Queensland Museum* 33(2): 645-649. Brisbane. ISSN 0079-8835.

Embryos at the germ disk stage were investigated by electron microscopy in *Achaearanea japonica* (Theridiidae) and *Neoscona nautica* (Araneidae). In both spiders, the germ disk was composed of spherical cells, which had almost no large yolk granules. In the inner part of the embryo, several large yolk granules were packed by cell membrane with various organelles and glycogen granules similarly to lycosid spiders. In *Achaearanea japonica* there were very flat cells which possessed several large yolk granules in the surface region where the germ disk was not formed. In *Neoscona nautica* cells were not observed in that region at all, so the packages of large yolk granules were exposed directly to perivitelline space. The araneid type can be distinguished from the agelenid and theridiid type.

Die Embryonen von *Achaearanea japonica* (Theridiidae) und *Neoscona nautica* (Araneidae) im Stadium der Keimscheibe wurden mittels des Elektronenmikroskops untersucht. Die Keimscheiben der beiden Spinnen bestanden aus sphärischen Zellen, die große Dotterkörnchen nur selten hatten. In dem inneren Teil von dem Embryo wurden manche großen Dotterkörnchen mit verschiedenen Organellen und Glykogenkörnchen von der Zellmembran gepackt, wie im Falle von den lycosiden Spinnen. Im Falle von *Achaearanea japonica* gab es sehr flache Zellen, die manche großen Dotterkörnchen hatten, in dem oberflächlichen Bezirk, wo die Keimscheibe nicht gebildet wurde. Im Falle von *Neoscona nautica* wurden die Zellen in dem Bezirk schließlich nicht beobacht, also waren die Packe von großen Dotterkörnchen direkt in der Perivitellinhöhle entblößt. Der araneide Typus soll sich von dem ageleniden Typus und dem theridiiden Typus unterscheiden. □*Spider, Achaearanea, Neoscona, embryo, germ disk, morphology.*

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Three types of germ disk formation are known in the embryos of spiders. In the most common type known in Agelenidae, the germ disk is formed on a hemisphere of the egg as the result of transformation of squamous blastoderm cells in this region into spherical cells. Egg surface of the other hemisphere is covered with squamous cells (Holm, 1952). In the second type known in Theridiidae, the most blastoderm cells converge on the germ disk region and few cells remain on the other hemisphere (Montgomery, 1909). In the third type found in many Araneidae, a rip appears in the blastoderm, so the yolk mass is exposed (Sekiguchi, 1957). Then all blastoderm cells take part in germ disk formation, and any cells are not observed in the region where the germ disk is not formed. A comparative study of the spider embryos at germ disk stage was carried out under light microscope (Kondo and Yamamoto, 1975). The study of germ disk formation under electron microscope was executed in lycosid spiders, whose germ disk formation is the agelenid type (Kondo, 1969, 1970). We had to examine whether remaining cells connect each other or not in theridiid type and whether extreme thin cells exist or not at the superficial region where the germ disk is not formed in araneid type. In present study, electron microscopic investigation of the embryos at germ disk stage was carried out in *Achaearanea japonica* and *Neoscona nautica*.

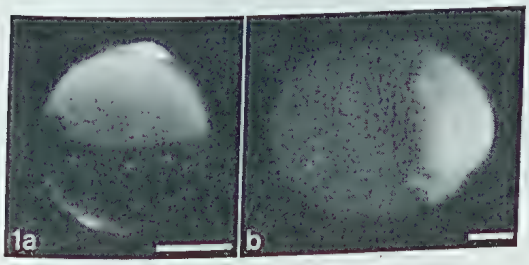
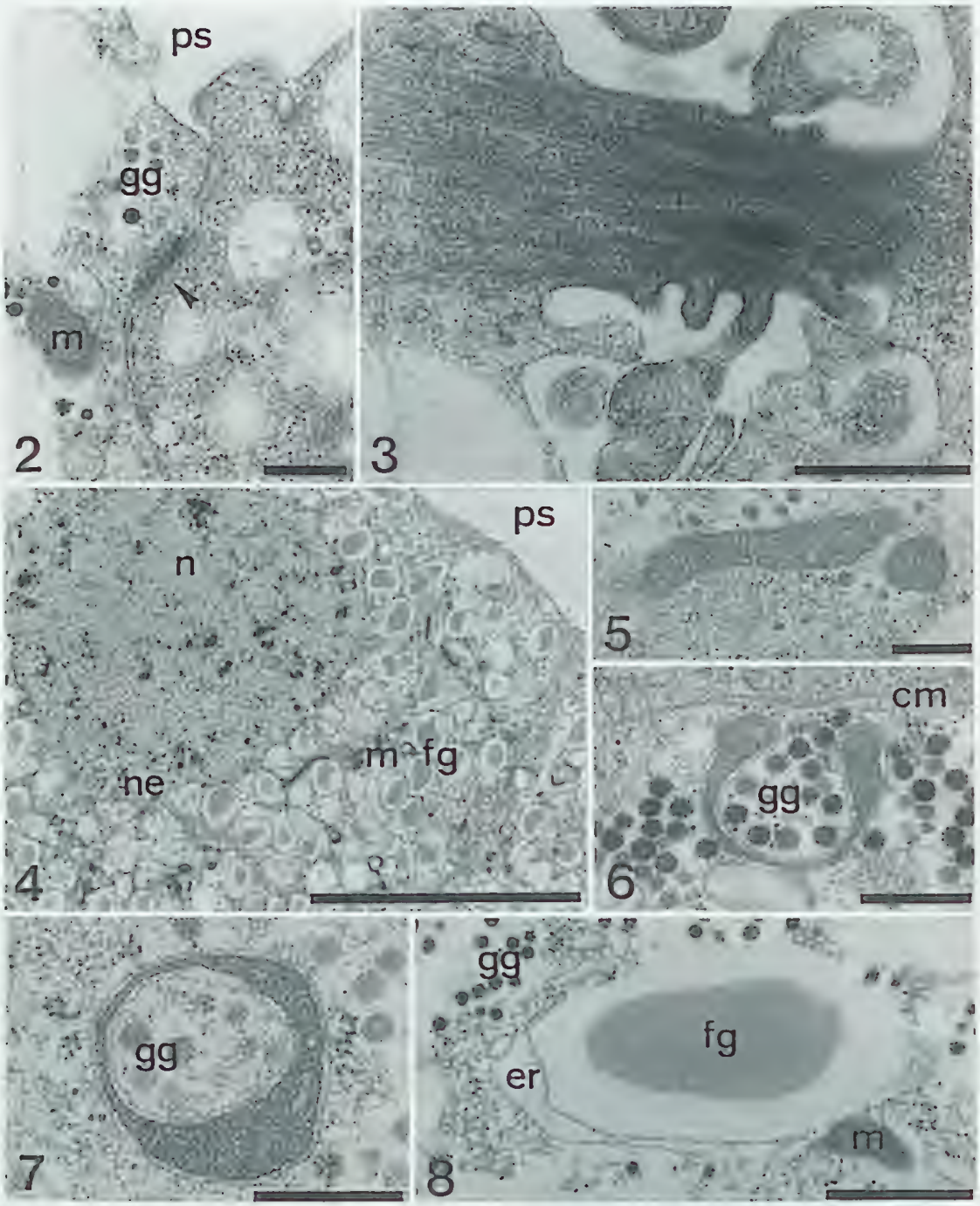


FIG. 1. The embryo at germ disk stage in *Achaearanea japonica* (a) and *Neoscona nautica* (b). In *A. japonica*, a few cells are found on region where germ disk is not formed. In *N. nautica*, exposed yolk mass is found on that region. Scale=0.2mm.



FIGS. 2-8. 2. *A. japonica.* Peripheral region of two germ disk cells. (0.5μm.) Arrowhead: Desmosome-like structure, 3. A mid-body. Many microtubules. (1μm.) 4. A germ disk cell. Main components of cytoplasm are fatty granules (fg) with medium electron dense matrix, and no large yolk granules. (10μm.) n: nucleus, ne: nuclear envelope. 5. Mitochondria have high electron dense matrix and the cristae are found faintly. (0.5μm.) 6. Cup-shaped mitochondrion. (0.5μm). cm: cell membrane. 7. Ring-shaped mitochondrion. (0.5μm.) 8. Fatty granule (fg) lacking complete limiting membrane, but partly enclosed by smooth-surfaced endoplasmic reticulum (er). (1μm.) gg: glycogen granules, m: mitochondria, ps: perivitelline space. Scales in parentheses.

MATERIALS AND METHODS

Achaearanea japonica (Bösenberg and Strand) (Theridiidae) and *Neoscona nautica* (L. Koch) (Araneidae) were used here. In *A. japonica*, the eggs collected in August were used. In *N. nautica*, the eggs laid in glass tubes at laboratory were used. The observation of the live eggs was carried out in liquid paraffin, where the opaque chorion became transparent. The eggs were fixed for 3 hours at 4°C in 2% paraformaldehyde and 2.5% glutaraldehyde solution in 0.1M phosphate buffer, pH 7.4, containing 0.2M sucrose. Through fixation, the eggs were cut in half with a tungsten needle. After rinsing more than one hour with the same buffer containing 0.2M sucrose, the samples were postfixed for one hour at 4°C in 2% osmic acid in 0.1M phosphate buffer, pH 7.4, without sucrose. After rinsing with the same buffer without sucrose, samples were dehydrated in ethanol series, transferred to propylene oxide, and embedded in Quetol-812. Ultrathin sections were cut on a ultra-microtome, LKB-4800, stained with uranyl acetate and lead citrate, and examined under Hitachi HU-12A electron microscope. Thick sections were prepared simultaneously, and stained with methylene blue for light microscopy.

RESULTS

Achaearanea japonica

The eggs were spherical and 0.5mm in diameter. Typical theridiid type germ disk formation was observed (Fig. 1a). At 25°C, the eggs took 24 hours to the germ disk stage after oviposition.

The germ disk was formed as a single layer composed of spherical cells, but the cells piled up in its central region. The diameter of germ disk cells was about 30μm, and that of nuclei was about 15μm. Desmosome-like structures were observed between germ disk cells at the superficial region (Fig. 2), but interdigitations were not observed. Mid-bodies were observed rarely (Fig. 3). Narrow cytoplasmic bridge connected cells adjacent to each other, and contained many microtubules.

The main components of cytoplasm were fatty granules, 1- 3μm in diameter, with a matrix of a medium electron density (Figs 4, 8). The limiting membrane was often obscure. The germ disk cell had almost no large yolk granules. Fine yolk granules, less than 5μm in diameter, were observed.

Mitochondria had a high electron dense matrix, and the cristae were found faintly (Fig. 5). Many figures of mitochondria showed oval or curved bars, and several showed cups (Fig. 6) or rings (Fig. 7).

Smooth-surfaced endoplasmic reticula were often found enclosing fatty granules (Fig. 8). Rough-surfaced endoplasmic reticula were not observed.

Typical Golgi bodies were rare. Vesicles were generally observed in the cytoplasm. The glycogen granules, 0.1μm in diameter, were very high electron dense, and scattered.

The superficial region where the germ disk was not formed was occupied by remaining flat cells. These cells were about 100μm in length, about 25μm in thickness at the central part, but often less than 1μm near the peripheral one (Fig. 9). The diameter of nuclei was about 13μm. Desmosome-like structures were observed between remaining cells (Fig. 9).

Several large yolk granules occurred in these remaining cells. The largest yolk granule was 20μm in diameter. Vesicles were sometimes arranged along the large yolk granules (Fig. 10).

The interior of the embryo was filled with yolk packages composed of several large yolk granules, various organelles and glycogen granules, and enclosed by cell membrane (Fig. 11).

Neoscona nautica

Ellipsoidal eggs of *N. nautica* had longer axis measuring 1.2mm and shorter axis measuring 1mm. At 23°C, 45 hours were needed from oviposition to establish the germ disk (Fig. 1b).

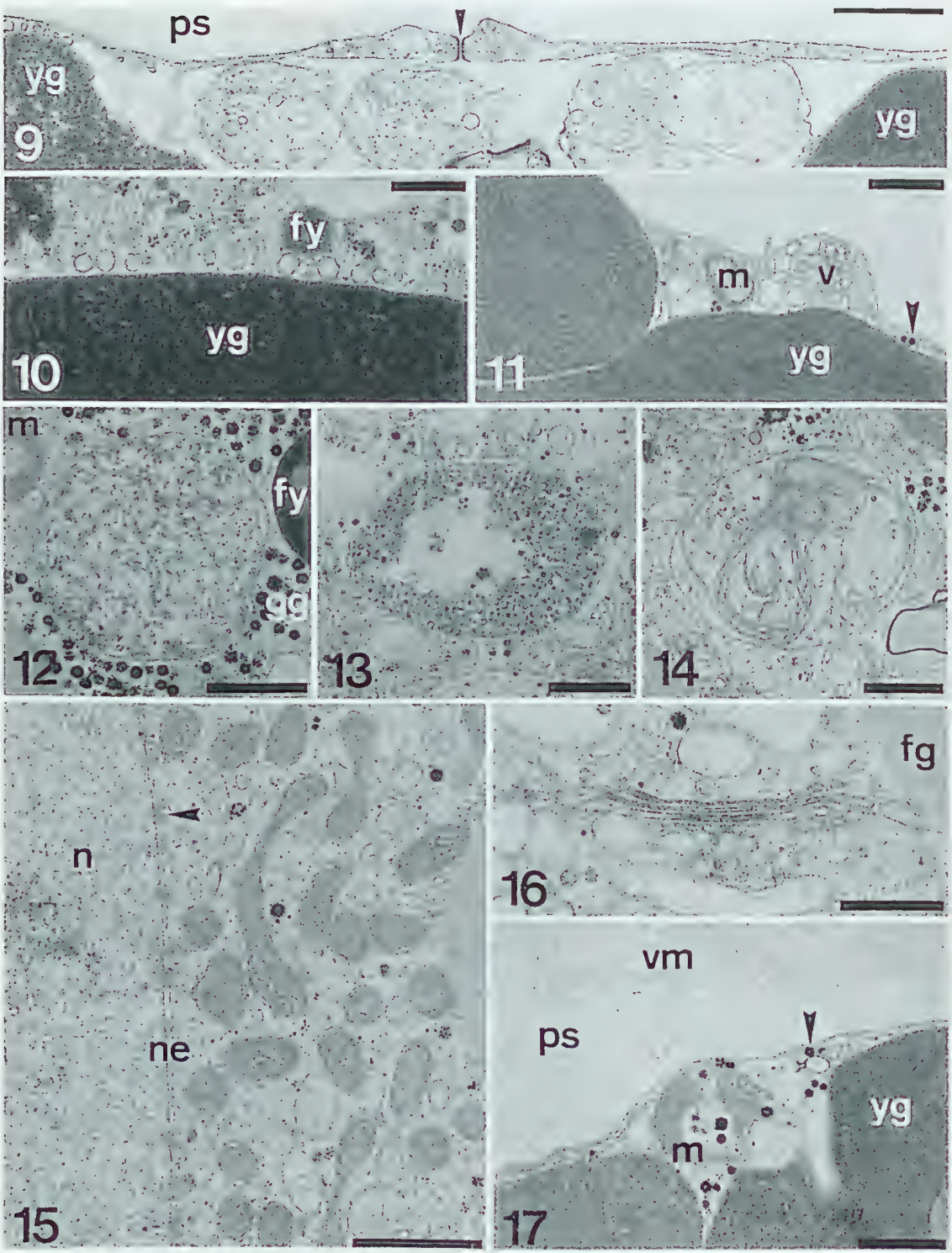
The germ disk was a single layer of spherical cells, but the cells piled up in its central region. The cell diameters were about 45μm, and those of nuclei were about 20μm. Between these cells, there were desmosome-like structures but no interdigitations.

Various types of lysosome-like bodies were observed (Figs 12-14). Mitochondria often crowded around the nucleus (Fig. 15). Several Golgi bodies were observed (Fig. 16). Other components of cytoplasm were similar to those of *A. japonica*.

No blastoderm cells were observed in the surface region where the germ disk was not formed (Fig. 17).

DISCUSSION

In this study, some cup- or ring-shaped



mitochondria were observed. These types of mitochondria were not reported in the embryos of lycosid spiders (Kondo, 1969, 1970), but they were figured in embryo of *A. tepidariorum* (Suzuki and Kondo, 1991). In *N. nautica*, many mitochondria were found surrounding the

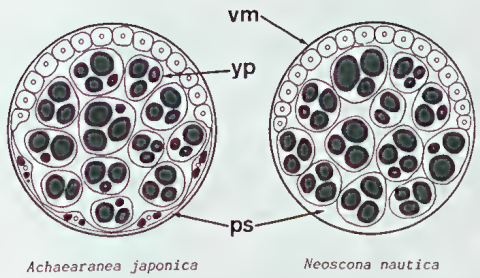


FIG. 18. Schematic figures of embryos at germ disk stage in *A. japonica* (left) and *N. nautica* (right). In both spiders, the germ disk is composed of spherical cells, which have almost no large yolk granules. The interior of the embryos is filled with yolk packages (yp). In *A. japonica*, there are very flat cells which possess several large yolk granules in the surface region where the germ disk is not formed. In *N. nautica*, any cells are not found in that region, so the yolk packages are exposed directly to perivitelline space (ps). vm: vitelline membrane.

nucleus. This phenomenon was reported in lycosid spiders (Kondo, 1969). In *N. nautica*, many lysosome-like bodies, described also in lycosid spiders (Kondo, 1969), were observed, however histochemical studies are needed for final identification.

In both spiders, *A. japonica* and *N. nautica*, interdigitations were not observed, but they were reported in germ disk region of lycosid spiders (Kondo, 1970).

In the inner part of the embryo in both spiders, several large yolk granules were packed by cell membrane with various organelles and glycogen granules. These structures were described as yolk spheres in lycosid spiders (Kondo, 1969). Since nucleus was not observed in them, these packages of large yolk granules were distinguished from yolk cells. In this investigation, detailed observation of yolk cells was not carried out.

The embryo at germ disk stage in *A. japonica* had very flat cells with several large yolk granules (Fig. 18). Distinct differences of cytoplasm were not observed between spherical germ disk cells and flat remaining cells. As in *A. tepidariorum* (Suzuki and Kondo, 1991), except for the large yolk granules and extreme flat shape in the remaining cells, the fine structure of embryo at germ disk stage in *A. japonica* was similar to that in lycosid spiders belonging to agelenid type.

In *N. nautica*, the yolk packages were exposed directly to the perivitelline space (Fig. 18).

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FIG. 9-17. 9-11. *A. japonica* 9. Extreme flat shape in peripheral part of remaining cells. A desmosome-like structure (Arrowhead) is found between cells. (1μm). 10. A large yolk granule included in remaining cell. Arranging vesicles along yolk granule. (0.5μm). 11. Peripheral part of yolk package in inner part of embryo. Large yolk granules, a ring-shaped mitochondrion (m), vesicles (v), and glycogen granules (arrowhead) are packed by cell membrane. (1μm).
12-17. *N. nautica* 12. A lysosome-like body including amorphous matrix. A ring-shaped mitochondrion (m) is found. (1μm). 13. A lysosome-like body including many small vesicles. (1μm). 14. A lysosome-like body including several double membranes or myelin-like structure. (1μm). 15. Mitochondria around nucleus (n) showing nuclear pore (arrowhead) and nuclear envelope (ne)(1μm). 16. A Golgi body. (0.5μm). 17. Superficial region where germ disk is not formed. A yolk package composed of large yolk granules (yg), a cup-shaped mitochondrion (m), glycogen granules (arrowhead), and vesicles are exposed directly to perivitelline space (ps). (1μm). Abbreviations: fg: fatty granule, fy: fine yolk granule, gg: glycogen granules; ps: perivitelline space, yg: yolk granule, vm: vitelline membrane. Scale line in parentheses.

AN EXPERIMENT ON COLONIZATION OF KARAKURT (*LATRODECTUS TREDECIMGUTTATUS*, BLACK WIDOW SPIDER) ON ISLAND TERRITORIES IN KAZAKHSTAN

CHINGIS K. TARABAEV

Tarabaev, C.K. 1993 11 11: An experiment on colonization of karakurt (*Latrodectus tredecimguttatus*, Black Widow spider) on island territories in Kazakhstan. *Memoirs of the Queensland Museum* 33(2): 651-652. Brisbane. ISSN 0079-8835.

To create an artificial, controllable population of *Latrodectus tredecimguttatus* (karakurt) with the aim of collecting venom, an experiment on mass colonisation of southern population spiders on an island territory was carried out. Retardation of the overwintering stage under laboratory conditions ensured the availability of large numbers of karakurt for colonisation and eliminated its uncontrollable reproduction in neighbouring territories.

Pour créer une population artificiele bien contrôlée des *Latrodectus tredecimguttatus* (karakurt) dans le but d'obtenir du venin on a mis une expérience de la dissémination des Araignées de la population méridionale sur le territoire insulairs. Le delai du stade hivernant dans les conditions de laboratoire assure la stabilisation du nombre de masse de karakurt pour leur colonisation et élimine leur reproduction non-contrôlée sur les territoires adjacents.

□*Colonisation, karakurt, egg sacs, Latrodectus.*

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In Kazakhstan, mass annual collections of venom-producing arachnids are carried out to obtain their venom for medicinal and other purposes. Black widow spiders ('karakurt', *Latrodectus tredecimguttatus* (Rossi)) are caught in the greatest numbers. At the same time, their abundance varies from year to year: quite often periods occur during which one can hardly find a single specimen (see Marikovskij, 1956; Levi, 1983; Tarabajev, 1990). A bite from a karakurt is an appreciable danger. Hence, during periods of great abundance, it must be controlled. In connection with this problem, we carried out an experiment on karakurt colonisation on an island with the aim of creating an abundant and controllable artificial population.

MATERIALS AND METHODS

The experiment was performed on the small island 'Malyj' (1.4km^2) in Alakol' Lake (46°08'N, 81°52'E) near the northern border of the known karakurt distribution: the 2nd instar spiderlings emerging from egg sacs are often affected here by the late frosts which occur in April-May (Tarabajev, 1990). In contrast, the development of spiders is critically restricted by the shortened warm season: if the postembryos within the egg sacs have no time to develop into the overwintering 1st instar spiderlings, they die during winter (Marikovskij, 1956). This phenomenon stipulated the possibility of creating a numerous, yet controllable karakurt population. To do so we retarded the development of spiderlings and then released the 2nd instars over the island. As a result, the spiderlings avoid the disastrous late frosts but the postembryos of the new generation in their egg sacs would not have time to develop into overwintering 1st instar spiderlings. This phenomenon is therefore the necessary condition for the possibility of creating a controllable karakurt population, as well as for elimination of uncontrollable mass reproduction of spiders on the neighbouring territories. For the intensification of degree-days deficit effect, the spiderlings from 500 egg sacs of *Latrodectus tredecimguttatus* collected in Uzbekistan (southern population from Dzhizak Steppe) were used in our experiment. Before the colonisation we made a census of the native population of karakurt on the island.

During winter, egg sacs of southern population spiders with overwintering first instar spiderlings were kept in the laboratory (temperature 0-5°C). In the second half of May these were placed into a gauze-covered 20 litre vessel at room temperature (18-22°C), for their reactivation from winter diapause. After moulting in their egg sacs, many spiderlings emerged; then the vessel which contained them was placed in a refrigerator (4-5°C) until June.

Before mass colonisation, a census of the natural karakurt population on 'Malyj' Island was carried out by the visual investigation of the

whole island territory fit for the settling by the southern population spiders of karakurt (ca. 8500 m^2).

RESULTS

While making a census of the native karakurt population on 'Malyj' Island before mass colonisation on 12 June 1988, we found one nest from the previous year with two empty egg sacs, and two more old nests. Six living karakurt specimens of 4-5th instar were also found. By late August there were 3726 nests from the southern population, or one specimen per 2-3m^2. Three females of the native karakurt population were also found: they differed by their larger size (no females were measured). In 28 nests of southern population spiders there was only one egg sac per nest: no egg sacs were found in the rest, while in three nests of native population spiders there were two egg sacs in each. Dissection of egg sacs confirmed our views. In four egg sacs of the native karakurt population there were postembryos, in two there were first instar spiderlings, while only eggs were found in 20 egg sacs of the southern population.

Of 100 nests examined in May 1989, 74 nests were without egg sacs–some nests were ruined; 26 nests each had one egg sac, all eggs were dead. These results confirmed that due to the artificially retarded development of southern population spiders in the northern conditions of Alakol' Lake the eggs had died within the egg sacs as they had insufficient time to develop to the overwintering first instar spiderlings (the average Alakol' area temperature in September is no more than 10-15°C).

We therefore propose the following scheme for the creation of many controllable artificial black widow populations for the purpose of obtaining venom.

In August-September, mass collection of females must be carried out. These females are kept in collection boxes for 2-3 weeks until they lay their egg sacs in these boxes. (This phenomenon was first noticed by us when studying the technique of mass collecting from the field). Females are subsequently used for obtaining venom while egg sacs are kept at room temperature until the 1st instar spiderlings emerge (overwintering stage). After that the egg sacs must be kept in a refrigerator at 0-5°C until the following season.

After the reactivation of spiderlings in spring, they are released over the island, which they recolonised effectively. Every August-September, mass collection of females is carried out, and the cycle is renewed.

Thus, the indubitable advantage of our method is the elimination of uncontrollable mass reproduction of karakurt and the absence of any necessity of special egg sacs collecting for colonisation.

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DISTRIBUTION OF *LATRODECTUS* (THERIDIIDAE), *ERESUS* AND *STEGODYPHUS* (ERESIDAE) IN KAZAKHSTAN AND CENTRAL ASIA

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Tarabaev, C.K., Zyuzin, A.A. and Fyodorov, A.A. 1993 11 11: Distribution of *Latrodectus* (Theridiidae), *Eresus* and *Stegodyphus* (Eresidae) in Kazakhstan and Central Asia. *Memoirs of the Queensland Museum* 33(2): 653-657. Brisbane. ISSN 0079-8835.

The distributions of three *Latrodectus* species (*L. tredecimguttatus*, *L. dahli* and *L. pallidus*), and of three eresid species (*Eresus niger*, *E. tristis* and *Stegodyphus lineatus*) within the Kazakhstan-Central Asian region are analysed based on the literature and on original data. *Latrodectus tredecimguttatus* presumably occupies almost the entire Kazakhstan territory, while two other widow species are local and more southern: both of them are first recorded here within Kazakhstan. Preliminary morphological and mating analyses show that both '*Latrodectus tredecimguttatus*' and '*Eresus niger*' within the territory of Kazakhstan and Central Asia are composite species: the first consists of at least one species different from the European *L. tredecimguttatus*, and the second consists of at least three separate species. On a analysé la distribution de trois espèces du genre *Latrodectus* (*L. tredecimguttatus, L. dahli* et *L. pallidus*) et de trois espèces de la famille Eresidae (*Eresus niger, E. tristis* et *Stegodyphus lineatus*) dans la région du Kazakhstan et de l'Asie centrale d'après le données littéraires et originales. L'aire d'habitation de *Latrodectus tredecimguttatus* comprend, hypothétiquement, presque tout le territorie du Kazakhstan, tandis que deux autres espèces sont locales et plus méridionales: l'une et l'autre sont mentionnées ici pour la première fois pour Kazakhstan. L'analyse morphologique préalable et les expériences d'accouplement montrent que *Latrodeetus tredecimguttatus* aussi bien que *Eresus niger* au Kazakhstan et à l'Asie Centrale sont des espèces collectives: dont la première se compose, au moins, d'une espèce différente de *L. tredecimguttatus* d'Europe et l'autre se compose, au moins, des trois espèces séparées.□*Latrodectus, Eresus, Stegodyphus, distribution.*

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The genus *Latrodectus* (Theridiidae) and the family Eresidae have not been studied very much in Central Asia. Before 1950 only one *Latrodectus* species was known from the former territory of the U.S.S.R.–*L. tredecimguttatus* (Rossi), or 'karakurt'. Two years later, Spassky (1952) first reported *L. pallidus* O. Pickard-Cambridge from the western, desert regions of the Turanian zoogeographic province [=Turkmenistan territory]. Later Charitonov (1954) described the new subspecies *L. pallidus pavlovskii* from Turkmenistan (the so-called 'white karakurt'). Twenty years later Tystshenko and Ergashev (1974) found in Uzbekistan another black widow species, *L. dahli* Levi. Amongst the Eresidae, three species have previously been recorded: *Eresus niger* (Petagna), *E. tristis* Kroneberg and *Stegodyphus lineatus* (Latreille).

This paper deals with new collections and data relating to the two groups and species distributions. Also, we suggest that previous broad species concepts, especially within *L. tredecimguttatus* and *E. niger*, must be revised.

MATERIALS AND METHODS

This work is based on material collected mainly by us in Kazakhstan and Central Asia. Our specimens were compared with those from Europe and North Africa. Spiders were examined in 70% alcohol using binocular microscopes MBS-1 and MBS-10. Preliminary experiments on mating between European *L. tredecimguttatus* and Widows from Kazakhstan were also carried out.

Abbreviations: BIN, Biological Institute, Novosibirsk, Russia; IZA, Institute of Zoology, Alma-Ata; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts, USA; MNHN, Muséum National d'Histoire Naturelle, Paris, France; ZISP, Zoological Institute, St. Petersburg; ZMMU, Zoological Museum of the Moscow University.

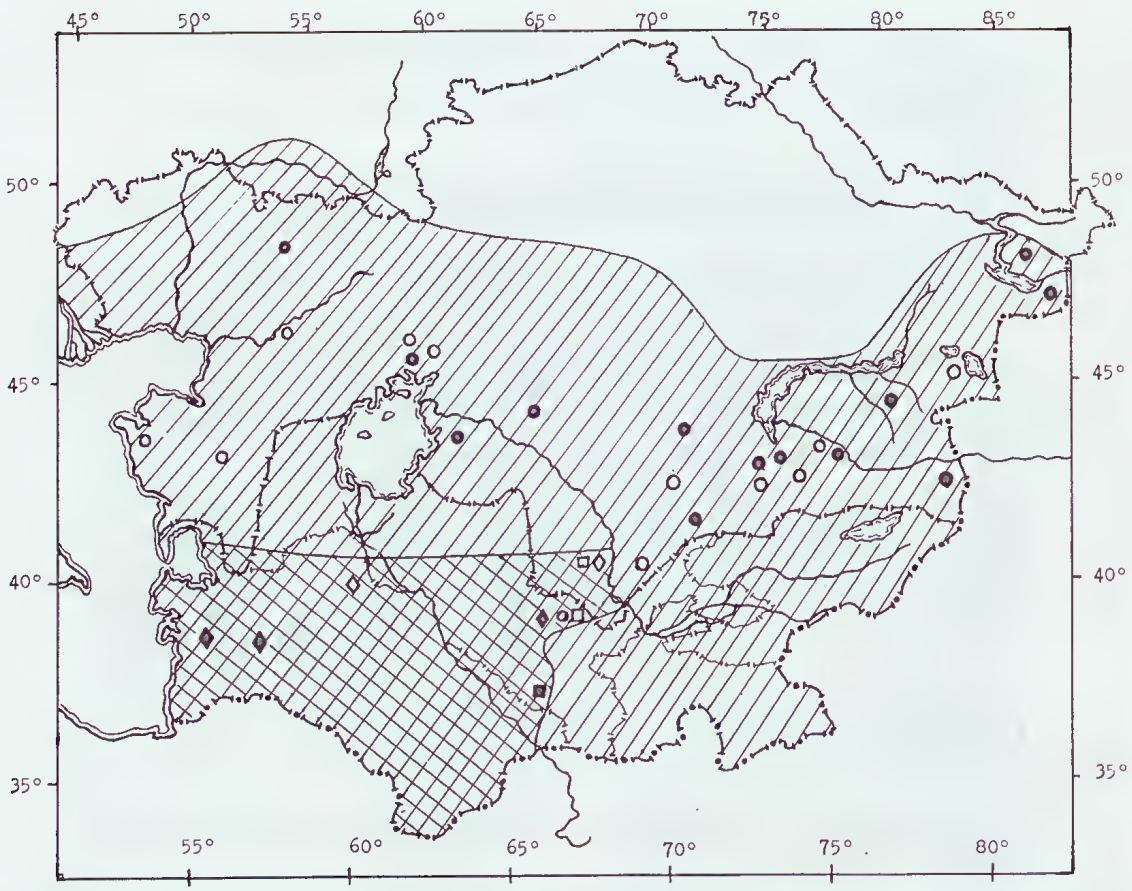

FIG. 1: Distribution of *Latrodectus* spp. in Kazakhstan and other Central Asian Republics. Legend: ○= *L. tredecimguttatus*; □= *L. dahli*; ◇ = *L. pallidus pavlovskii*; oblique hatching = distribution of *L. tredecimguttatus* after Marikovskij (1956); cross hatching = suggested distribution of *L. pallidus* within the distribution of *L. tredecimguttatus*. Black figures = published data; white figures = original data.

RESULTS AND DISCUSSION

FAMILY THERIDIIDAE

Latrodectus Walckenaer

REMARKS

The northern border of the widow spiders' distribution within the former USSR seems to pass near 52°N (Fig. 1).

Latrodectus tredecimguttatus (Rossi)
'Karakurt'

REMARKS

Within the former USSR this species has been known under the names *L. conglobatus* C.L. Koch, *L. erebus* Savigny and Audouin, *L. lugubris* Motchoulsky, *L. tredecimguttatus* var. *lugubris* (Dufour), etc. (Charitonov, 1932). Rossikov (1904) devoted a monograph to this species and Marikovskij (1956) analysed the biology and distribution of *L. tredecimguttatus* within the former USSR. According to this author, karakurts are found over almost all of Kazakhstan (Fig. 1). However, existing difficulties in the systematics of *Latrodectus* species (see Levi, 1983), as a rule, result in too wide an interpretation of their distribution. When investigating *Latrodectus* species, we found that adult females of *L. tredecimguttatus* from Italy had a light spotted abdomen while Kazakhstan specimens were completely black. Dr G. Schmidt (pers. comm.) considers the karakurt from Kazakhstan to be the species *Latrodectus lugubris* (Dufour) described from Egypt. Preliminary experiments on mating carried out in 1991 together with Mr D. Weickmann-Zwoerner (Germany) showed that

Kazakhstan specimens could not cross with European *L. tredecimguttatus* (two males from Kazakhstan were used).

At present the distribution of *L. tredecimguttatus* as delimited by Marikovskij (1956) must be revised, as we now suppose the traditional '*L. tredecimguttatus*' in Kazakhstan to be a separate species.

Material Examined

Italy: 3 ♀, Lazio, near Priverno, 16 May 1962, fields and stones, H. Levi (MCZ). Kazakhstan and Central Asia: many males and females from different localities (IZA).

Latrodectus dahli Levi

Remarks

This very localised species among the Central Asian republics occurs in Uzbekistan only (Tystshenko & Ergashev, 1974; Ergashev, 1990); in Kazakhstan, it was found by us first in the Kyzylkum Desert (two females, det. Dr Y.M. Marusik)(Fig. 1). We have compared our specimens with the female paratype of *L. dahli* from Iran and found their resemblance in the hairiness of the abdomen's dorsum (long slender spines and rather long setae between them: see also Tystshenko and Ergashev, 1974, fig. 3). Nevertheless, the epigynal opening in all our specimens is 4 times as wide as long, while in the female paratype it is only 3.4 times as wide as long; slight differences are also in the vulvae (cf. Levi, 1959, figs 11, 12; Tystshenko and Ergashev, 1974, figs 4, 5). As the male of *L. dahli* from the type locality is up to now undescribed, we cannot be sure that our specimens belong to real *L. dahli*.

Material Examined

Iran: 1 paratype ♀, Bushire, Persian Gulf (MCZ). Uzbekistan: 1 ♂, 1 ♀, Kashkadarja Area, Karshi Steppe, N.E. Ergashev. Kazakhstan: 2 ♀, South Kazakhstan Area, Kyzylkum Desert, 77.5k NW of Chardara Vill., 5-6 Jun 1989, Tarabaev, Fyodorov, Zyuzin (IZA).

Latrodectus pallidus pavlovskii Charitonov
(Fig. 1)

Remarks

Within Kazakhstan, it was found by us first in the Kyzylkum desert, which is probably its northernmost limit. To clarify the taxonomic position of *L. pallidus pavlovskii*, thorough comparison of our spiders with the type material or topotypes of *L. pallidus* is necessary.

Material Examined

Turkmenistan: 1♀, Tashauz Area, Shakhsenem, under *Artemisia*, 9 Oct 1983, O.S. Soyunov. Uzbekistan: 4 ♀, Dzhizak Area, 'Kyzylkum' state farm, 16 Jul 1982, N.E. Ergashev. Kazakhstan: 1♀, South Kazakhstan Area, Kyzylkum Desert near Tabakbulak Vill., 24 Aug 1991, A.A. Zyuzin, B.M. Gubin (1 ♂, 2 ♀ of Tabakbulak population in laboratory) (IZA).

Family Eresidae

Eresus Walckenaer

Eresus niger (Petagna)

Remarks

Published and original data on the distribution of this species within the Sibero-Kazakhstan-Central Asian region, in the European part of Russia (see Charitonov, 1932) and in Europe (see Bonnet, 1956) show that the northern limit of its area seems to pass near 56°N: thus, *E. niger* is theoretically distributed over the whole Kazakhstan and the Central Asian region. Preliminary analysis of material we have at our disposal show that at least three separate species of the '*Eresus niger*' complex occur in Kazakhstan (Fig. 2). The acute deficit of specimens of both sexes taken from the same place is the main obstacle to a detailed taxonomic study.

According to Merrett and Millidge (1992), the correct name for the species *Eresus niger* (Petagna) is *Eresus cinnaberinus* (Olivier) (see also Lehtinen, 1967, p. 233).

Material Examined

France: 2 ♂, 2 ♀ 2 juv., Col du Ceris, 15 Sep 1908; Banyuls, 31 May 1909 (MNHN, No. AR 838). Spain: 3 ♂, 4 ♀, La Granja, Jun 1908 (MNHN, No. AR 837). Mongolia: 1 ♂, 'Potanin, Schenkel det. 1946' (MNHN, No. AR 852). Hungary: 1 ♂, Csákberény, Vertes, 20 Sep 1991, V.V. Dubatolov, V.G. Mordkovitch. Russia: 3 ♂, Bashkir Reserve, Bashart, I.V. Stebaev; 1 ♂, Novosibirsk Area, 13k W of Karasuk Vill., 7 Sep 1989; 5 ♂, ibidem, 27k SE of Zdvinsk Vill., Malyje Chany Lake, 10 Sep 1989, V.P. Pekin. Turkmenistan: 1 ♂, Kopetdag Reserve, 15 May 1988, Karpenko; 2 ♂, 25 Aug 1988, ibidem, 15k W of Firyuza Vill., Mount Dushak, 2100 m; 1 ♂,

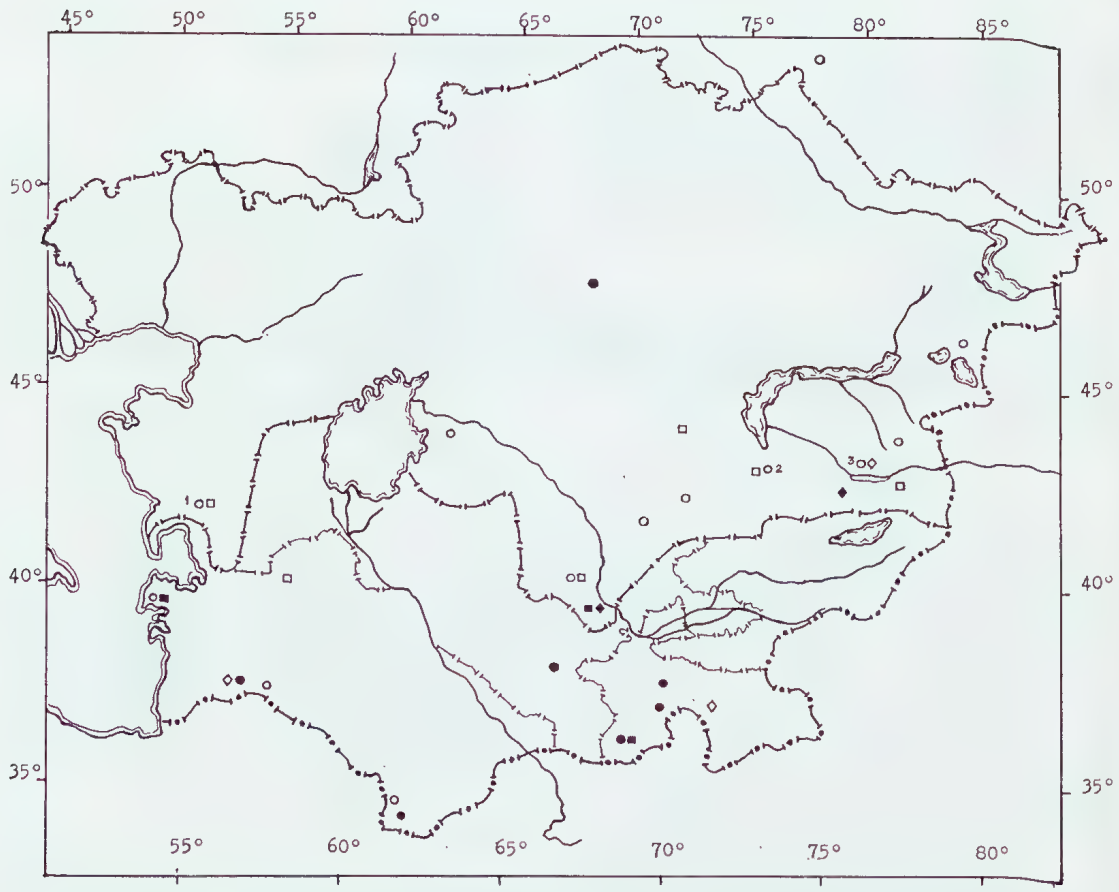

FIG. 2: Distribution of eresid spiders in Kazakhstan and other Central Asian Republics. Legend: ○= '*Eresus niger*' complex: 1, 2, 3, = *E.* sp. 1, 2, 3 (see text); ◇=E. tristis; □= *Stegodyphus lineatus*. Black figures = published data; white figures = original data.

ibidem, Firyuza Vill., 3 Apr 1991, V.V. Dubatolov, V.K. Zinchenko; 1 ♂, Kugitang Range, 5k SE of Bazar Depe Vill., 13-19 May 1991, V.V. Dubatolov (all BIN). Kazakhstan: numerous ♂♂♀♀ from different parts of Kazakhstan (see Fig. 2) (IZA).

Eresus tristis Kroneberg

Remarks

According to published data, this species was previously found only in southern and South-Eastern Kazakhstan (Kroneberg, 1875; Spassky and Shnitnikov, 1937); beyond the borders of the former USSR, *E. tristis* was found only in China by G.N. Potanin's expedition: see Simon (1895), 'la riv. Sotschshan au N. de la chaîne du Tjan-Shan'. [Charitonov (1932) wrongly placed this site within the former USSR territory].

Males of *E. tristis* can be readily separated from those of *E. niger* by the black colour of their abdomen and legs (as in *E. niger* females), sometimes with white markings. Despite this very distinctive feature, *E. tristis* was recently synonymised with *E. niger* based on the similarity of their genitalia (see Nenilin and Pestova, 1986). However, our preliminary data showed sufficient differences of *E. tristis* from all of our 'red' males in the fine structure of the male palp; at the same time, black males from different parts of Kazakhstan and Central Asia have very similar palp structure. The main taxonomic problem is that the female of this species is up to now unknown.

Material Examined

Kazakhstan: 1 ♂ holotype, South Kazakhstan Area, 'Syrdarja, the end of April', A.P. Fedtschenko's Turkestan Scientific Expedition by the Natural History Amateurs' Society (ZMMU No. Ta 1104); 1 ♂, Alma-Ata Area, 5k NE of Kapchagaj City, A.A. Fyodorov (IZA).

Turkemistan: 3 ♂, Western Kopetdag Ridge, near Kara-Kala Vill., 7 Feb 1979, I. Morozova (ZISP). Tadzhikistan: 1 ♂, 'turn to Chashma, 9.V.1986, Itka' (BIN).

Stegodyphus Simon

Stegodyphus lineatus (Latreille) (=*Eresus arenarius* Kroneberg)

Remarks

This species was previously known from Turkmenistan, Uzbekistan and Southern Kazakhstan. We have found it considerably northwards and eastwards (Fig. 2).

Material Examined

Many males and females from: Spain; Italy (Sicily); Algeria; Tunisia (Kairouan) (MNHN No. AR 785, 786); different parts of Kazakhstan and Central Asian republics (see Fig. 2) (IZA).

ACKNOWLEDGEMENTS

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GEOGRAPHIC VARIATION OF THE NUMBER OF B-CHROMOSOMES IN *METAGAGRELLA TENUIPES* (OPILIONES, PHALANGIIDAE, GAGRELLINAE)

N. TSURUSAKI

Tsurusaki, N. 1993 11 11: Geographic variation of the number of B-chromosomes in *Metagagrella tenuipes* (Opiliones, Phalangiidae, Gagrellinae). *Memoirs of the Queensland Museum* 33(2): 659-665. Brisbane. ISSN 0079-8835.

Chromosomes of *Metagagrella tenuipes* (L. Koch) (Arachnida, Opiliones, Phalangiidae, Gagrellinae) were surveyed in 8 populations in Japan. Almost every individual examined had one or more (highest number per cell was 19) supernumerary or B-chromosomes, in addition to the basic set of chromosomes (2n=18). These B-chromosomes are heterochromatic, and during meiosis they appear to behave as univalents. The number of B-chromosomes varied both among and within populations. The number also fluctuated to some extent among cells from the same individual, suggesting nondisjunction at mitotic anaphases. No correlation could be elucidated between the number of B-chromosomes and external morphologies or habitat type. The number of B-chromosomes may affect growth rate, and in turn reduce the synchrony of breeding within a population.

Die Chromosomen von *Metagagrella tenuipes* (L. Koch) (Arachnida, Opiliones, Phalangiidae, Gagrellinae) wurden in 8 japanischen Populationen untersucht. Fast jedes überprüfte Individuum wies eines oder mehrere (die höchste Anzahl pro Zelle war 19) überzählige oder B-Chromosomen zusätzlich zum Standardchromosomensatz (2n = 18) auf. Diese B-Chromosomen sind heterochromatisch und scheinen sich während der Meiose als Univalente zu verhalten. Die Zahl der B-Chromosomen variiert sowohl zwischen als auch innerhalb von Populationen. Sie schwankt in gewissem Ausmaß auch zwischen Zellen aus ein und demselben Individuum, was auf Non-Disjunction bei mitotischen Anaphasen schließen läßt. Zwischen der Anzahl der B-Chromosomen und der äußeren Morphologie oder Habitattypen konnten keine Korrelationen gefunden werden. Es besteht die Möglichkeit, daß die Zahl der B-Chromosomen die Wachstumsrate beeinflussen und in der Folge die Synchronie der Fortpflanzung innerhalb einer Population reduzieren kann.□*Opiliones, Metagagrella tenuipes, Japan, B-chromosomes, geographic variation.*

Nobuo Tsurusaki, Department of Biology, Faculty of Education, Tottori University, Tottori 680, Japan; 29 October, 1992.

The harvestman *Metagagrella tenuipes* (L. Koch) is widespread throughout Japan but with a peculiar habitat and distribution pattern. In southern Japan, this opilionid is typically coastal. However, in northern Japan, it also occurs inland and prefers open habitats, e.g. parks and gardens, that are affected by moderate human disturbance.

During a chromosomal survey of this species, the number of chromosomes varied both within and among populations, with a range of 2n=18 to 36. Moreover, the number of chromosomes varied somewhat from one cell to another in almost all individuals. Close examination of mitotic and meiotic chromosomes revealed that the karyotype of this species is usually composed of 2n=18 standard chromosomes and one or more supernumerary or B-chromosomes, and that the latter cause the overall chromosome number to vary. Here, I will describe the karyotype, nature of the B-chromosomes, and pattern of geographic variation in the B-chromosome number.

MATERIALS AND METHODS

The specimens used for chromosome examination are listed (Table 1, Fig. 1). Cytological data were obtained from air-dried preparations of testes or ovaries of field-collected adults and penultimates. The technique used is described in Tsurusaki (1985) and Tsurusaki and Cokendolpher (1990). In some cells, patterns similar to C-bands were observed despite the fact that these cells had received no special treatment. In many individuals the number of B-chromosomes varied from cell to cell. In such cases, the chromosome number of each is represented by a modal number.

For two populations (Nakajima and Maruyama), lengths of femur I of the specimens used in the chromosome preparation were measured with an eyepiece graticule.

Detailed collection data on the specimens examined are listed in the appendix.

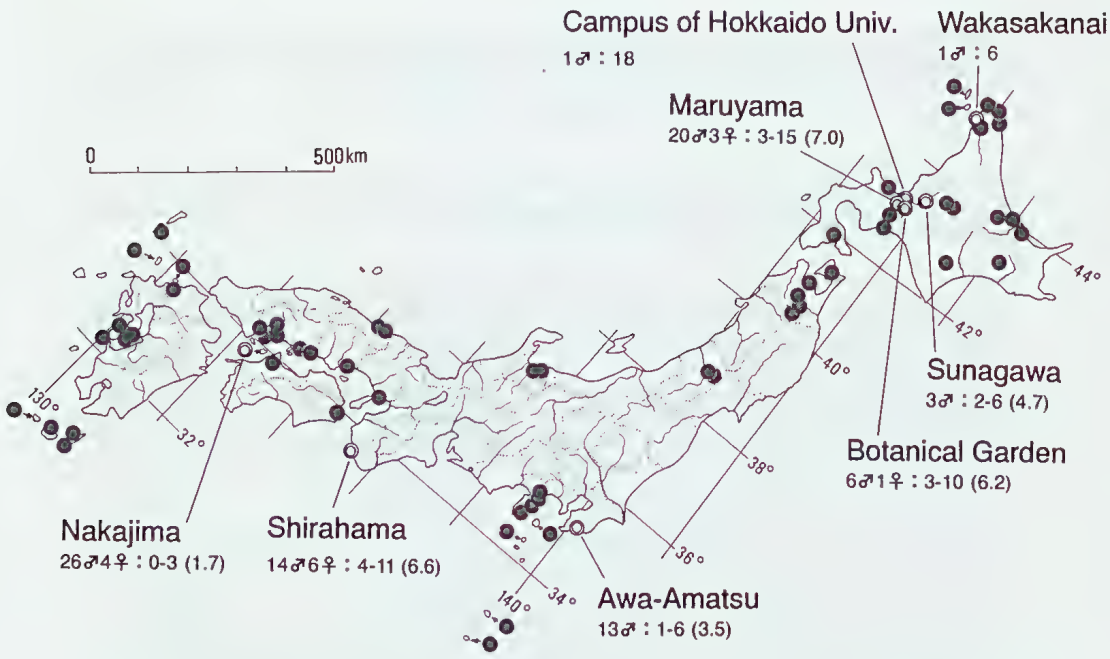

FIG. 1. Map of populations of *M. tenuipes*, Japan, used here (double open circles) with records compiled from literature (e.g. Suzuki, 1973; Suzuki and Tsurusaki, 1983) and data in the appendix (solid circles). No. of samples and range of B-chromosome number in each study population are shown, with means in parentheses.

RESULTS

Karyotypes and Nature of B-Chromosomes

The chromosome number of this species varied enormously among and within populations. From comparisons of the karyotypes of individuals with the lowest chromosome number, 2n=18, to those from others with 2n=19 and greater, and from analyses of both meiotic chromosomes and unintentionally obtained C-banded chromosomal spreads, the chromosome number of the standard karyotype, which consists of so-called A-chromosomes alone, was determined to be 2n=18 for both males and females (Figs 2-3).

1. Standard karyotype (Fig. 3)

Autosomes consist of 8 pairs of medium-sized metacentrics (Nos. 4 and 5), submetacentrics (Nos. 1, 3, 7, 8), and subtelocentrics (Nos. 2 and 6). The X chromosome, the largest, is subtelocentric, while Y is submetacentric and similar in size to chromosome No. 1. In C-banded mitotic metaphases, centromeric regions of the A-chromosomes were positively stained (Figs 4-5). No prominent differences were found among the

TABLE 1. B-chromosome numbers in 8 populations of *Metagagrella tenuipes*. NOTES: [1] S = seashore habitats, I = inland habitats e.g. parks, fields; [2] Range, mean and mode not for all cells counted but for values represented by mode of each individual; [3] Calculated only for samples with >5 individuals; [4] One or more were juveniles.

Locality and habitat type in parentheses[1]	Date	Specimens examined	Number of B-chromosomes[2]				
			min.	max.	mean	mode	SD[3]
Wakasakanai (S)	9-IX-1985	1 ♂[4]	6	6	6	6	-
Sunagawa (I)	8 & 15-X-1986	3 ♂	2	6	4.7	6	-
Campus of Hokkaido Univ. (I)	18-IX-1981	1 ♂	18	18	18	18	-
Botanical Garden, Sapporo 1982 (I)	5-IX-198	5 ♂, 1 ♀	4	10	6.2	4	2.40
as above, 1986 (I)	8-VIII & 9-IX-1986	8 ♂, 2 ♀	3	9	6.2	5, 7, 8	1.93
Maruyama, Sapporo (I)	5-IX-1986	20 ♂, 3 ♀	3	15	7.0	6	2.75
Awa-Amatsu (S)	27-VIII-1984	13 ♂	1	6	3.5	4	1.39
Shirahama (S)	29-VII-1983	14 ♂, 6 ♀[4]	4	11	6.6	6	1.60
Nakajima (S)	26-VIII-1986	26 ♂, 4 ♀	0	3	1.7	1, 2	1.02

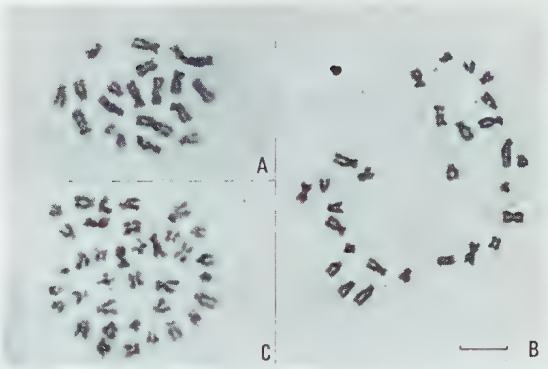

FIG. 2. Representative chromosome complements at spermatogonial mitotic metaphase of male *Metagagrella tenuipes*. A, Nakajima, 2n=18 (18A's); B, Maruyama, 2n=28 (18A's + 10B's); C, campus of Hokkaido Univ., 2n=37 (18A's + 19B's). Scale = 5μm.

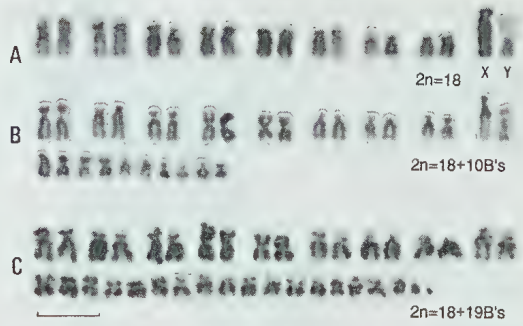

FIG. 3. Karyotypes of male *Metagagrella tenuipes* based on the photographs in Fig. 2. A, Nakajima; B, Maruyama; C, campus of Hokkaido Univ. B-chromosomes are arranged on the second row in B and C. Scale = 5μm.

standard karyotypes of individuals from various populations.

2. B-chromosomes

In addition to a set of standard chromosomes described above, almost all chromosomal spreads contained at least one B-chromosome. These were meta- or submetacentric, equal to or smaller than the shortest pairs (No. 8) of the A-complement (Fig. 3). In C-banded chromosome spreads, the B's were heteropycnotic, darkly staining along their total lengths (Figs 4-5). During meiosis, the B's remained univalent (Fig. 4-5) even when the cell carried 2 or more. The number of B's varied considerably from one cell to the other within a single individual, possibly due to nondisjunction at anaphase during mitosis.

Numeric variation in B's among individuals within populations was also evident (Fig. 6). No significant differences were found in the number of B's between the sexes from any population (Mann-Whitney U-tests for each of four populations where both sexes were sampled, P=0.48-0.96).

Geographic Variation in Number of B's

The number of B-chromosomes varied significantly among populations (single classification ANOVA: F=34.6; d.f.=7; P<0.001) (Figs 1 and 6, Table 1). The lowest and the highest population means of the number of B's were 1.7 for Nakajima (n=30) and 18 for the campus of Hokkaido University (n=1), respectively, and the means of the other populations lay between the two extremes, range = 3.5-7. However, no significant correlations could be detected between the number of B's and characteristics such as latitude (Spearmann's coefficient of rank correlation, r_s=0.19, n=8, P>0.05) and habitat types (seashore or inland: Mann-Whitney U-test, P>0.05).

DISCUSSION

Characteristics of the B-Chromosomes

According to Jones and Rees (1982), B-chromosomes have been reported in over 1000 species of plants and more than 260 species of animals. In Arachnida, however, only three species of Acari have been shown to have B's: *Aponomma fimbriatum* and two species of *Haemaphysalis* (Oliver and Bremner, 1968; Oliver *et al.*, 1974).

The B-chromosomes in *Metagagrella tenuipes* have the following characteristics that are typical for B's recorded in various other organisms (White, 1973; Jones and Rees, 1982; Werren *et al.*, 1988; Shaw and Hewitt, 1990; Jones, 1991): (1) they are smaller than most members of the A-complement; (2) they appear to be comprised of a large amount of constitutive heterochromatin; (3) they remain univalent during meiosis; (4) the number of B's varies from one cell to another even within an individual, indicating they display nondisjunction at anaphases of spermatogonial mitoses.

However, the frequency and the number of B's were rather unusual. In this species, every population sampled contained B's and the frequency within a population was up to 87% in Nakajima and 100% in the other 7 populations. The number of B's retained per individual of this species was also extraordinarily high; the population means had a range from 3.5 to 7 in 6 out of 8 populations

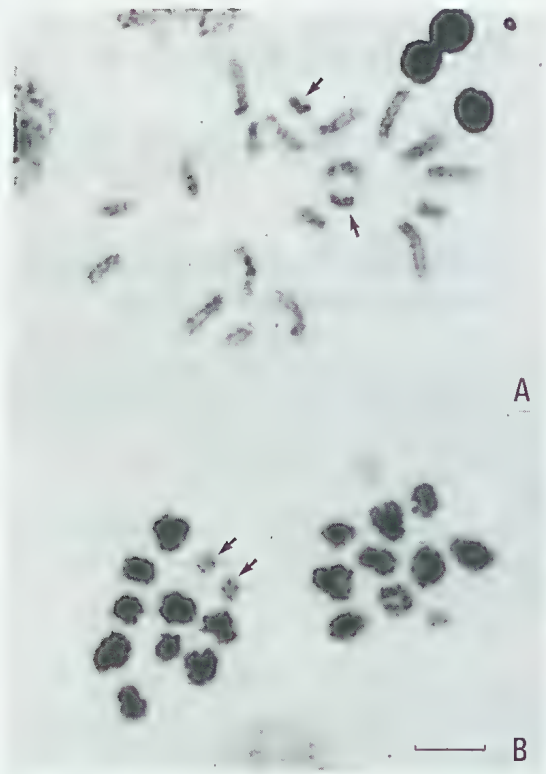

FIG. 4. C-banded mitotic metaphase (A) and meiotic metaphase I (B) in ♂ *M. tenuipes* from Sunagawa, with 2 B-chromosomes (arrowed). Scale = 5μm.

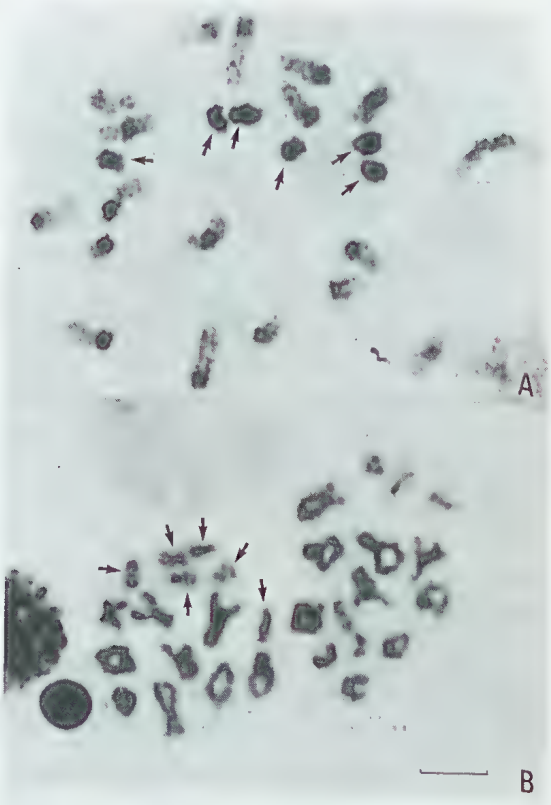

FIG. 5. C-banded mitotic metaphase (A) and diakinesis - metaphase I (B) in ♂ *M. tenuipes* from Maruyama, with 6 B-chromosomes (arrowed). Note: 9 bivalents formed by 9 pairs of A-complement of chromosomes. Scale = 5μm.

(Table 1). The higher end was found in the single male sampled from the campus of Hokkaido University, whose modal number of 18 B's was exhibited by 30 cells and the maximum number of 19 in 3 cells (Figs 2-3). These are among the highest numbers of B's in animal species so far recorded, close to the number 'about 20' in *Xylota nemorum* (Diptera: Syrphidae) (Boyes and Van Brink, 1967).

Effect of B's on Phenotype

Metagagrella tenuipes shows marked variation both among and within populations in external morphology, such as body size, leg lengths, degree of development of a spine on the dorsal scutum, number of noduli on the legs, and coloration of the body (Suzuki, 1973; Suzuki and Tsurusaki, 1983). However, no correlation was found between these characters and the number of B-chromosomes (Fig. 7). These facts are consistent with the observation that the B's are C-band positive. If these B's are indeed genetically inactive, numerical variation of B's would lead to no effect on the phenotype of their owner.

Although few studies have demonstrated any exophenotypic effect due to B's, some show a relationship between the number of B-chromosomes and the rate of development (Hewitt and East, 1978; Harvey and Hewitt, 1979). Thus, there is a possibility that the presence of B-chromosomes retards the cell cycle due to the additional DNA or its organization which is possibly different from A-chromosomes. In turn, these effects may influence the growth and development of the whole organism (Jones and Rees, 1982). Such influences might be related to an unusual feature of the life history of this species, namely, high variability among individuals in the time to reach maturity. The duration of coexistence of juveniles and adults of this species at Maruyama is estimated to be about three weeks, whereas it is less than 1-2 weeks in other species of opilionids having no B-chromosomes, such as *Oligolophus aspersus*, *Leiobunum japonicum*, and two species of *Nelima* from the same locality (Tsurusaki,

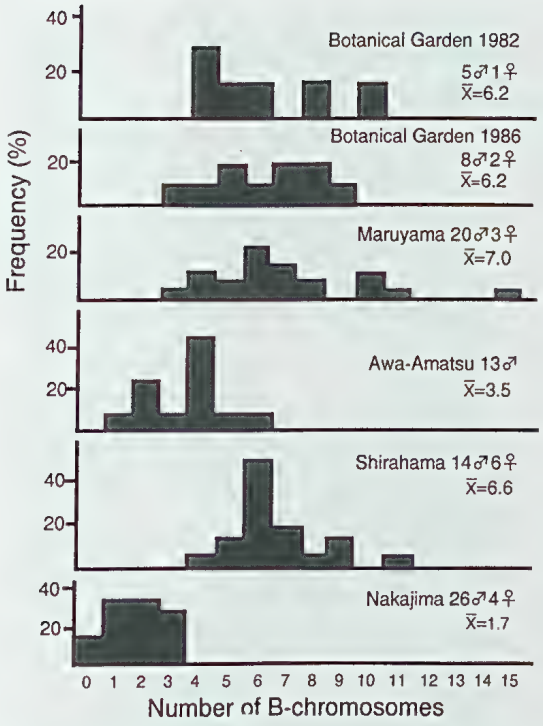

FIG. 6. Frequency distribution of B-chromosome numbers in 6 samples from 5 populations. The other 3 populations (Wakasakanai, Sunagawa, and campus of Hokkaido Univ.) omitted due to paucity of specimens surveyed.

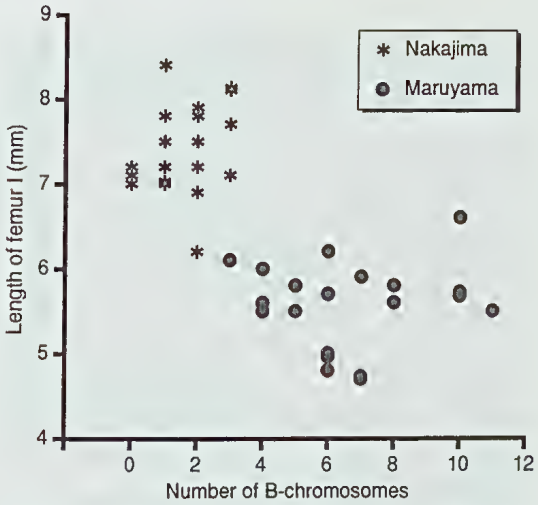

FIG. 7. Relation of length of femur I to number of B-chromosomes in 2 populations (Nakajima and Maruyama) of *M. tenuipes*. No significant correlation between 2 variables in each population [r = 0.305 (P>0.1) for Nakajima; r = 0.065 (P>0.1) for Maruyama], although both characters show prominent differences between two populations. Two variables may be negatively correlated (although spuriously) between populations. Leg lengths decrease with increase in latitude (Tsurusaki, unpubl.) but the number of B's does not.

unpublished data based on weekly field-collections made in 1979). The same phenomenon is also inferred from field-data from various localities all over Japan. This versatility in the timing of final molting of this species might be ascribed to the numerical variation of B-chromosomes. Further study is needed.

Geographic Variation in Number of B's

The fact that the B's are found in every population over a wide geographic range of this species indicates that they are of rather ancient origin. Marked morphological variation among the B-chromosomes also attests to their long evolutionary history. However, it is also possible that they might be produced *de novo* from the A-complement by recurring mutation.

Although B's appear widespread across the species range, the number of B's considerably varied among populations, with a fairly wide range from 1.7 at Nakajima to 18 on the campus of Hokkaido University. In each population, the number of B's may be stable for at least several years; there was no significant difference in their frequencies in the Botanical Garden at Sapporo which were sampled in 1982 and 1986 (Fig. 6). If B-chromosomes were inherited in a non-Mendelian manner, and were neutral in phenotypic expression, the frequency of B's would not be stable. For example, it might be expected that the crossing of a male with 3 B's and a female with 3 B's would produce some offspring with 4 or more B's. However, no individuals with more than 3 B's are found in Nakajima population. This indicates that some selection pressure limits the number of B's that one individual can retain in a particular population. It is still uncertain what factors determine the population mean and the range of the number of B's. However, this species may be useful in studying various aspects of B's and 'selfish' DNA, including the controversial issues on the level of selection discussed by Werren *et al.*, (1988) and Shaw and Hewitt (1990).

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APPENDIX. New material of *M. tenuipes* used in Fig. 1. Data in order: locality, altitude if available and needed, no. individuals, no. specimens dissected in parentheses if needed (Value may not be as in Table 1, since no countable chromosomal spreads were obtained for some specimens), date collected, collector (NT = N. Tsurusaki; YN=Y. Nishikawa).

HOKKAIDO: I. Rebun, Kabukai, Kabukai Elementary School, 10m, 1 juv., 11-VIII-1990, YN. I. Rishiri: Oshidomari, ca. 20m, 1 ♂, 8-VIII-1985, Y. Kuwahara; Oshidomari, 5m, 1 ♀, 2 juv., 7-9-VIII-1990, S. Ueno, M. Sato, YN; Fujino, 10m, 1 juv., 7-VIII-1985, NT. Wakkanai: Soya Point, 1m, 2 ♂, 3 ♀, 1 juv., 2-IX-1988, NT; Wakkanai Port, 2m, 4 ♀, 5 juv., 7-VIII-1985, S. Ishimaru, NT. Esashi-gun, Hamatonbetsu-chô, Beniya-Genseikaen, 2 ♂, 1 ♀, 8 juv., 14-15-VIII-1990, YN, S. Ueno. Teshio-gun: Toyotomi-chô, Wakasakanai, on coastal sand dune: 1 juv. (1 juv.), 9-VIII-1985, NT; 1 ♂, 1 ♀, 1-IX-1988, NT, T. Tanabe. Toyotomi-chô, Toyotomi Spa, 2 ♂, 1 ♀, 1 juv., 12-13-VIII-1990, YN. Monbetsu-gun, Engaru-chô, Engaru JR Station, 2 juv., 30-VI-1985, NT. Kamikawa-gun, Tôma-chô, Tôma Cave, outside cave, 4 ♀, 29-30-VIII-1985, N. Yoshida. Sunagawa, On a bank of R. Penke-Utashinai, 1 ♂ (1 ♂), 8-X-1986; 2 ♂ (2 ♂), 15-X-1986, NT. Sapporo: campus of Hokkaido Univ., 1 ♂, 1 ♀, 18-IX-1981, NT; Botanical Garden of Hokkaido Univ.: 9 ♂, 9 ♀ (5 ♂, 1 ♀), 5-IX-1982, NT; 13 ♂, 16 ♀, 5-IX-1984; 7 juv. (7 juv.), 8-VIII-1986; 3 ♂ (3 ♂), 9-IX-1986, NT. Sapporo, Maruyama, 23 ♂, 19 ♀ (20 ♂, 3 ♀), 5-IX-1986, NT. Tomakomai, Tomakomai Experiment Forest of Hokkaido Univ., 1 ♂, 3 ♀, 19-IX-1980, NT. YAMAGATA PREF.: Obanazawa-shi, Obanazawa, 1 ♂, 1 ♀, 4 juv., 29-VIII-1983, A. Otaka; 6 ♂, 1 ♀, 4-X-1984, A. Otaka; Obanazawa-shi, along Route 347, 2 ♀, 9-X-1988, T. Tanabe. CHIBA PREF.: Awa-gun, Amatsu-Kominato-chô, Awa-Amatsu, Saneiri coast: 1 ♂, 1 ♀, 2 juv., 21-V-1983; 1 ♂, 18-IX-1983, K. Ishii; 2 ♂, 1 ♀, 18-XII-1983, K. Ishii. Awa-Amatsu, Saneiri, Matsugabana, under growth of maritime fern, *Cyrtomium falcatum*, 1-2m, 23 ♂, 21 ♀ (16 ♂), 27-VIII-1984, NT. TOKYO PREF.: I. Hachijo, Mine, 2 ♂, 2 ♀, 17-18-XI-1983, H. Okada. TOYAMA PREF.: Toyama-shi: Yokogoshi, 1 ♀, 20-X-1978; 1 juv., 18-V-1990, N. Nunomura; Hamakurosaki, *Pinus thunbergi* forest, 1 juv., 2-V-1979; 3 ♂, 1 ♀, 6-VIII-1980, N. Nunomura. WAKAYAMA PREF.: Nishimuro-gun, Shirahama-chô, Shirahama, Seto Marine Biological Lab., 1 ♂, 3 ♀, 10-VII-1983, S. Otsuka; 29 ♂, 41 ♀, 43 juv. (16 ♂, 1 ♀, 9 juv.), 29-VII-1983, NT. TOTTORI PREF.: Iwami-gun, Iwami-chô, Uradome coast, Kamogaiso, 4 ♂, 3 ♀, 7-IX-1988, NT, R. G. Holmberg; Ketaka-gun, Ketaka-chô, Yatsukami, Anedomari coast, 1 ♂, 3 ♀, 5-IX-1987, NT. OKAYAMA PREF.: Oku-gun, Ushimado-chô, Ushimado Marine Biological Station of Okayama Univ., Benten-iwa, 1 ♂, 4 ♀, 10-VIII-1983, T. Sato. HIROSHIMA PREF.: I. Nômi-jima, Irukanohana: 12 juv., 13-VI-1976; 1 ♂, 4-VII-1977, NT. EHIME PREF.: Onsen-gun, Nakajima-chô, I. Nakajima, Okushi: 3 ♀, 6-7-VIII-1971; 1 ♀, 13-VIII-1974, NT; Okushi, Seno-hana, 51 ♂, 69 ♀ (30 ♂, 6 ♀), 26-VIII-1986, NT. I. Nakajima: Himegahama, 1 ♀, 13-VIII-1974, NT; I. Takashima off Himegahama, 3 ♂, 3 ♀, 6-VIII-1971, NT. Matsuyama, Mt. Fukumi, Fukumiji, 860m, 2 juv., 6-IX-1970, NT. NAGASAKI PREF: Iki-gun, Ishida-chô, Kukishoku, 4 ♂, 5 ♀ , 2 juv., 20-VI-1990, M. Yamashita. KUMAMOTO PREF.: Ushibuka-shi, I. Tojima, 2 juv. M. Yoshikura; Amakusa-gun, Itsuwa-chô, Oniike, 3 ♂, 1 ♀ , 2 juv., 8-VII-1958, M. Yoshikura; Matsushima-chô, Aitsu, 4 ♂ , 1 ♀, 10-VIII-1957 M. Yoshikura; Matsushima-chô, I. Maejima, 2 ♂ , 4 ♀, 20-VII-1963, M. Yoshikura. KAGOSHIMA PREF.: I. Yakushima, Shiratani-Unsui-kyô to Mt. Miyanoura-dake, 1 ♀, 2-5-VIII-1983, H. Okada. I. Tanegashima: Hamada, 1juv., 11-VII-1983, Sk. Yamane; Makigawa, 3 juv., 3-5-V-1984, Sk. Yamane. Kumage-gun, Kamiyaku-chô, I. Kuchinoerabu-jima, 1 ♂, 27-IV-1984, Collector unknown.

MATING BEHAVIOUR AND FEMALE SPERM STORAGE IN *PHOLCUS PHALANGIOIDES* (FUESSLIN) (ARANEAE)

G. UHL

Uhl, G. 1993 11 11: Mating behaviour and female sperm storage in *Pholcus phalangioides* (Fuesslin) (Araneae). *Memoirs of the Queensland Museum* **33**(2): 667-674. Brisbane. ISSN 0079-8835.

Females of *Pholcus phalangioides* do not possess receptacula seminis but store transferred spermatozoa in their genital cavity. The spermatozoa are embedded in glandular secretion that is discharged from two accessory glands situated in the posterior wall of the genital cavity. The gland cells belong to a complex type of class 3 cells according to the classification of Noirot and Quennedy (1974, 1991). With the sperm mass of a single copulation the females are able to fertilize several batches of eggs, although the sperm might be easily washed out with the passage of the first batch of eggs (Forster, 1980). Nevertheless, females allow repeated copulations. The first copulation usually took over an hour but subsequent copulations lasted only a few minutes, no matter whether the female mated with the same or with a different male. Copulations after egg-laying tended to be long. Male spiders might achieve reproductive advantage in copulating with any female they meet and females might have an interest in filling up their storage capacities.

Pholcus phalangioides Weibchen besitzen keine Receptacula seminis im üblichen Sinne, sondern speichern die während einer Kopulation übertragenen Spermien im Hohlraum des Uterus externus. Die Spermien werden dort in ein Sekret eingelagert, welches von zwei akzessorischen Drüsen produziert wird. Diese Drüsen befinden sich in der posterioren Wand des Uterus externus. Die Drüsenzellen sind nach einem Klassifikationssystem, das für epidermale Drüsenzellen von Insekten erstellt wurde (Noirot and Quennedy, 1974, 1991), einem komplizierten Typ der Klasse 3 zuzuordnen. Mit den Spermien, die während einer einzigen Kopulation übertragen wurden, können die Weibchen mehrere Eigelege befruchten (Uhl, in press a), entgegen der Annahme, die Spermien könnten während der ersten Eiablage leicht ausgewaschen werden (Forster, 1980). Die Weibchen lassen dennoch mehrere Kopulationen zu, wobei die erste Kopulation gewöhnlich über eine Stunde dauert, jede weitere Kopulation schon nach wenigen Minuten abgebrochen wird, unabhängig davon ob es sich um das selbe oder um ein neues Männchen handelt. Nach einer Eiablage lassen die Weibchen wieder lange Kopulationen zu. Für die Männchen mag es von Vorteil sein sich mit jedem Weibchen zu paaren dem sie begegen, und Weibchen könnten ein Interesse daran haben ihre Speicherkapazität voll auszuschöpfen. □*Araneae, Pholcidae, Pholcus phalangioides, sperm storage, glands, secretion, ultrastructure, repeated matings, copulation duration.*

Gabriele Uhl, Institut für Biologie I (Zoologie), Universität Freiburg i.Br., Albertstraße 21a, 7800 Freiburg i.Br., Germany; 28 October, 1992.

Most female spiders store sperm within storage structures that are spatially separated from the genital cavity. Some 'primitive' spider families such as Diguetidae, Liphistiidae, Archaeidae and Pholcidae retain the sperm mass within the genital cavity itself (Forster, 1980). Forster assumed that the bursal storage mode has little survival value as the sperm mass gets flushed out with the passage of the eggs and therefore, storing the spermatozoa in spatially separated storage structures would eliminate the need for repeated insemination. Despite the bursal storage mode, female *Pholcus phalangioides* (Fuesslin) are able to fertizile numerous batches of eggs with the sperm of a single insemination (Uhl, in press a). However, the females probably do not rely on the amount and fertility of the spermatozoa transferred during a single copulation. This would be risky as the spermatozoa might be defective or insufficient. I expect the females to fill up their storage capacity by means of repeated matings at least after egg-laying when few clumps of spermatozoa remain in the genital cavity after oviposition. However, if the female does not have the opportunity to copulate repeatedly, the stored spermatozoa can be sufficient for fertilizing following egg batches successfully. This study will also give a brief morphological account on the bursal storage mode in *P. phalangioides* and will present histological and ultrastructural findings on the glandular tissue that exudes its product into

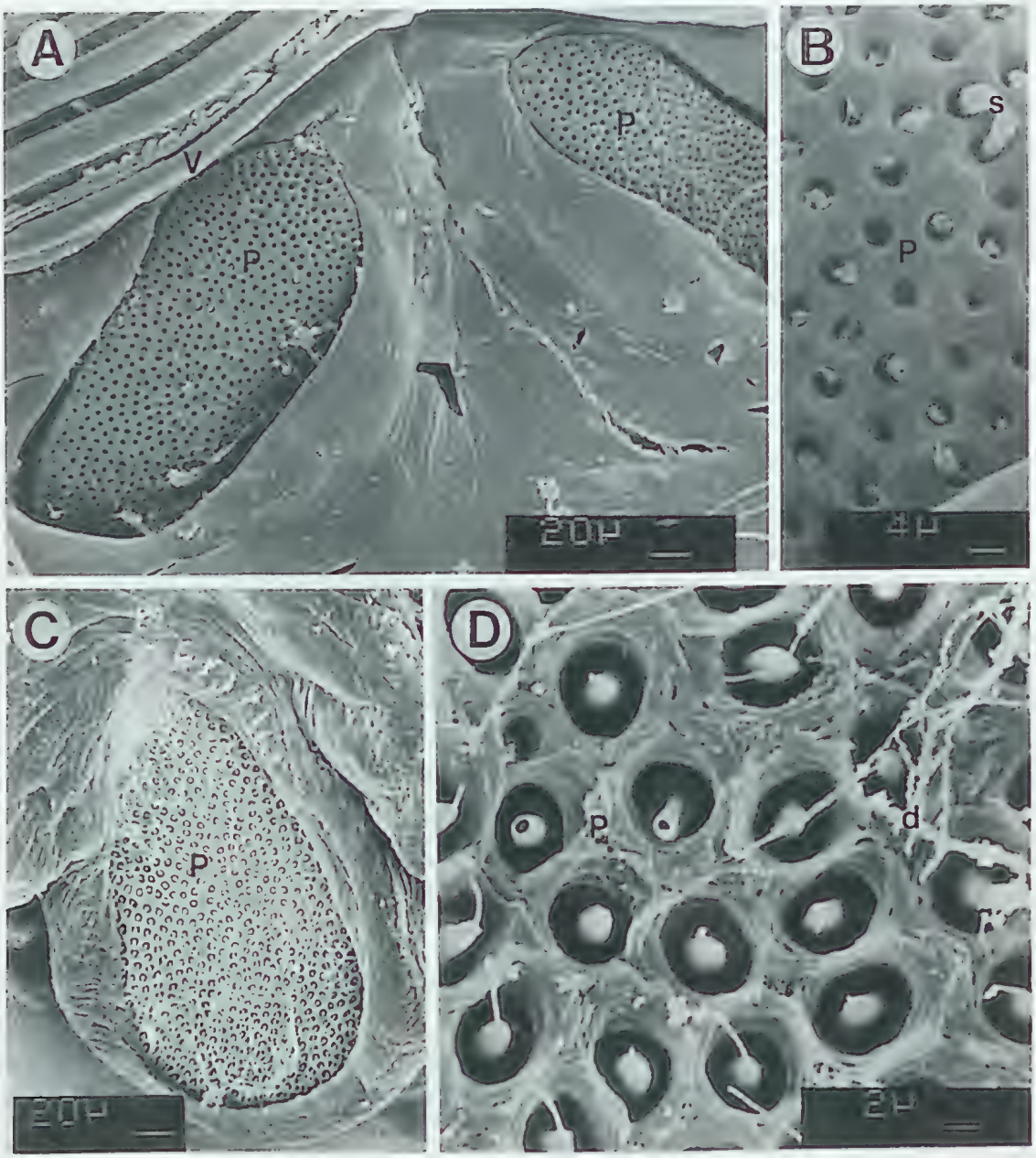


FIG. 1. Dorsal wall of genital cavity of *P. phalangioides*. A, Pore plates viewed from genital cavity; B, Pores that exude secretion, C, One pore plate from its dorsal side, glandular tissue removed; D, cuticular ductules of accessory glands.

the genital cavity for sperm storage. For more detailed information see Uhl (in press b, c).

MATERIAL AND METHODS

Juvenile *Pholcus phalangioides* were reared individually in the lab. To investigate mating behaviour the spiders were kept in couples in plastic boxes (16.5x9x6.5cm) and their behaviour was recorded day and night on video tape.

Five different experimental set-ups were used in order to answer the indicated questions:

1. Duration of copulation: Virgin females were offered unexperienced males.

2. Copulation duration with sperm-depleted males: Virgin females were offered recently experienced males (1/2 hour after termination of copulation).

3. Repeated matings with same partner: Previously virgin females were kept with previously unexperienced males for up to 20 days.

4. Repeated matings with changing partner: 1/2 hour after their first copulation females were offered unexperienced males.

In order to check the influence of box-size on mating behaviour 4 experiments were carried out using 2.5 times bigger boxes (18x12x11.5cm).

5. Duration of copulation after egg-laying: Post-oviposition females that had mated once were allowed to copulate again with unexperienced males.

For SEM studies adult females were anaesthetized, dissected and fixed in 70% ethanol or Bouin. In order to investigate the sclerotized parts of the female genital tract, the female genitalia were put in 5% NaOH solution until the soft parts were dissolved. Some genitalia were opened or cut with a sharp razorblade to locate the sperm mass in the genital cavity. They were dehydrated in ethanol, CP-dried, sputter coated with gold and examined in a Zeiss Semco Nanolab 7.

For light- and electron microscropy the spiders were anaesthetized and dissected in glutaraldehyde. After fixation in 2% osmium tetroxide/-glutaraldehyde, they were post-fixed in osmic acid (modified after Franke *et al.*, 1969), dehydrated in graded series of alcohol followed by propylene oxide and embedded in Epon. The semithin sections (0.7-1μm) were cut with glass knives on a Reichert OmU3 and stained with toluidin. Ultrathin sections were cut with glass knives and diamond knife. They were stained with uranyl acetate, counterstained with lead citrate and examined in a Zeiss EM9 electron microscope.

RESULTS

Mating Behaviour

1. Virgin females copulated with unexperienced males over an hour ($\bar{x}$=64.5 minutes; sd= 26.6; shortest duration: 16 min, longest duration: 122 min; n=42). This supports findings of Reagan and Reagan (1989) who investigated 104 pairs (mean copulation duration: 72.3 min; sd=43.3; shortest: 10 min, longest: 304 min).

2. Five males that had mated with virgin females (long copulation I) were brought half an hour after copulation to another virgin female. All copulations were long ($\bar{x}$: 56.8 minutes). The males probably refill their copulatory organs prior to the second copulation. The filling was observed in only one case by chance and was not detectable on the video recording.

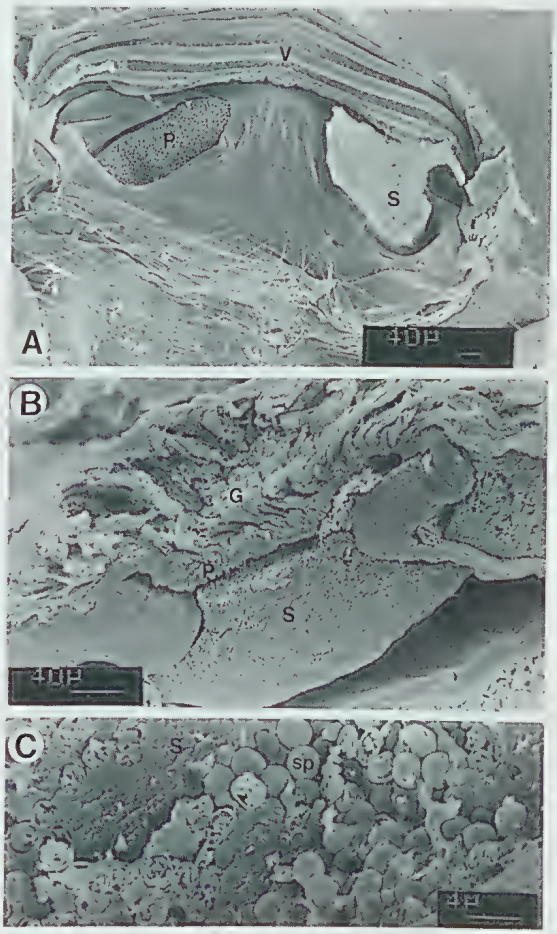


FIG. 2. A, Genital plate flipped back, dorsal wall of genital cavity revealed. Two pore plates, one concealed by secretory 'plug'; B, secretory 'plug' in genital cavity cut sagittally; C, Sperm mass in female secretion in female genital tract.

3. Unexperienced males and females were kept in pairs up to 20 days. Six females out of 12 allowed copulation from time to time: one female copulated twice, four females copulated 3 times, one female copulated five times. The second and the following copulations were always very short, they took only 2 to 5 minutes. Copulation duration tended to decrease in successive matings.

4. Unexperienced males were brought to females that had already mated once (long copulation I). In 9 of 14 cases the females allowed

Experimental set-up	n	Copulation duration (min.)
1. Virgin ♀ with unexperienced ♂	42	64.5 (16-122; 26.6)
2. Virgin ♀ with recently experienced ♂	5	56.8 (37-75; 13.9)
3. Second copulation with same ♂	6*	3.6 (2-5; 1.02)
4. Second copulation with unexperienced ♂	9*	2.6 (1.5-5; 1.0)
5. Post-oviposition ♀ with unexperienced ♂	7	59.6 (21-103; 31.4)

TABLE 1. Mating behaviour in *P. phalangioides* as a function of female reproductive history.* Only cases of copulation given. Range and standard deviation in parentheses.

further copulation. Again, second copulations lasted only a few minutes (1.5-5 min). Control experiments using bigger boxes showed that 3 females out of 4 allowed repeated matings (4.5; 2; 1 + 1 min).

5. Seven females that had mated once (long copulation I) and were kept separately afterwards, had access to males after oviposition. Copulation duration was long.

Copulation duration seems to depend on the reproductive history of the females (Table 1).

The Genital Cavity

The dorsal (posterior) wall of the genital cavity is characterized by two oval pore plates (Fig. 1A). The pore plates converge in direction of the ridges and grooves that make up the heavily sclerotized valve which separates the genital cavity from the oviducts. Both plates are perforated by pores of 3-5μm in diameter (Fig. 1B). The pores are in contact with gland cells that exhude their glandular secretions into the cavity (Fig. 1B).

The tissue-free pore plates reveal the canal zones of the glandular tissue when looked at from their dorsal side (Fig. 1C). Situated in cavities, cone-shaped hollow structures are apparent (Fig. 1D). These are the distal regions of the canals that open into the uterus externus as the pores of the pore plate. Proximally the canals change into thin ductules that exhibit a rough surface after 6-10μm (Fig. 1D).

Sperm Storage

The accessory glands discharge their products through the pores of the pore plates into the genital cavity and form two portions of secretory 'plugs'. (Fig. 2A). During copulation, the male transfers sperm mass into the female secretion (Fig. 2B). The spermatozoa are surrounded by individual secretory envelopes, they are coiled and inactive (Fig. 2C).

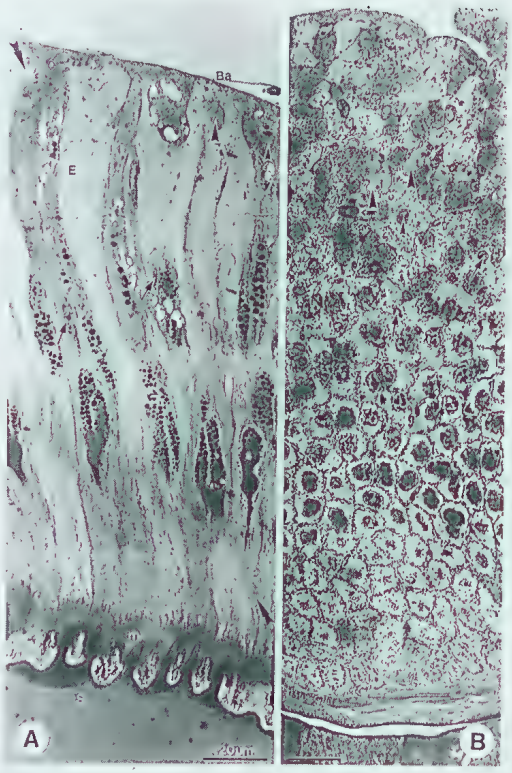


FIG. 3. Semithin section of accessory glands. A, Longitudinal section. Arrows mark nuclei of different cell types. Ba: basal lamina, E2: outer envelope cell, G: gland cell, m: microvilli, P: pore plate, s: secretion of the gland cells, S: secretion in genital cavity; B, Transverse section. Arrows and stars mark nuclei of different cell types. Scale lines: 20μm.

The Accessory Glands

The glandular tissue is composed of highly elongated cells (Fig. 3). Different cell types form the gland with various nuclei at different levels (Fig. 3A). The gland consists of lightly stained cells whose nuclei lie close to the basal lamina, and densely stained cells with more distal nuclei. Nuclei of other cell types lie mainly in the centre.

Secretory vesicles are apparent in the densely stained cells (the gland cells G). Accumulations of such vesicles are found in the apical second third of the glandular tissue. Each accumulation forms two portions of tightly packed secretory globules that discharge their contents into a common reservoir which is homogeneously coloured (Fig. 3A, B).

Bordering on the gland's orifices is a zone of

greyish coloration that is formed by the light coloured cells (outer envelope cells E2).

Histology and ultrastructure show that the glandular tissue includes many similar units, each provided with a cuticular ductule that leads to the pore plate (Fig. 3A). Each unit comprises two gland cells and two envelope cells. The two gland cells (G1, 2) join each other to form a common reservoir (Fig. 4, 5B). They are rich in granular endoplasmic reticulum (Fig. 5A), mitochondria and dense secretory vesicles and exhibit numerous golgi complexes in the supranuclear region. The vesicles vary in size (up to 1.5μm in diameter) and get more numerous in the distal cell region. They are enclosed in a close-fitting membrane which is obscured by the matching density of the mature granula. The inner envelope cell (E1) surrounds and partially separates the two gland cells (Fig. 5B, C, D) and forms the proximal part of the ductule (Fig. 4C). The outer envelope cell (E2) surrounds all of the previously mentioned cells. Its cytoplasm is poor in organelles (Fig. 5A, B, D). It produces the distal part of the ductule and forms numerous microvilli that gather round the ductule and the orifice (Fig.5E) and represent the greyish zone visible in the semithin section of Fig. 3A.

The gland cells and the outer envelope cell form a so-called basal labyrinth adjacent to the basal lamina (Figs 4, 5A). The glandular units are separated from each other by elongated epithelial cells.

DISCUSSION

The glandular units of the accessory glands in *P. phalangioides* belong to class 3 cells (Noirot and Quennedy, 1974, 1991). According to that classification, a gland cell is associated with a cuticular ductule that has been secreted by a 'canal' cell. In *P. phalangioides* however, there are two gland cells that are always connected by a common microvilli region, one inner and one outer envelope cell that form a double ensheathing of the gland cells. Moreover, both envelope cells take part in producing the canal that leads to the pore plate. Therefore, the glands studied here belong to a complicated type of class 3 cells.

There is some information on gland structures in female spider genitalia. The glands of the receptaculum seminis of Telemidae belong to class 1 type of gland cells (Lopez and Juberthie-Jupeau, 1983), and in some Theraphosidae De Carlo (1973) stated a class 1 composition. However, the light microscope study of Kovoor (1981) indi-

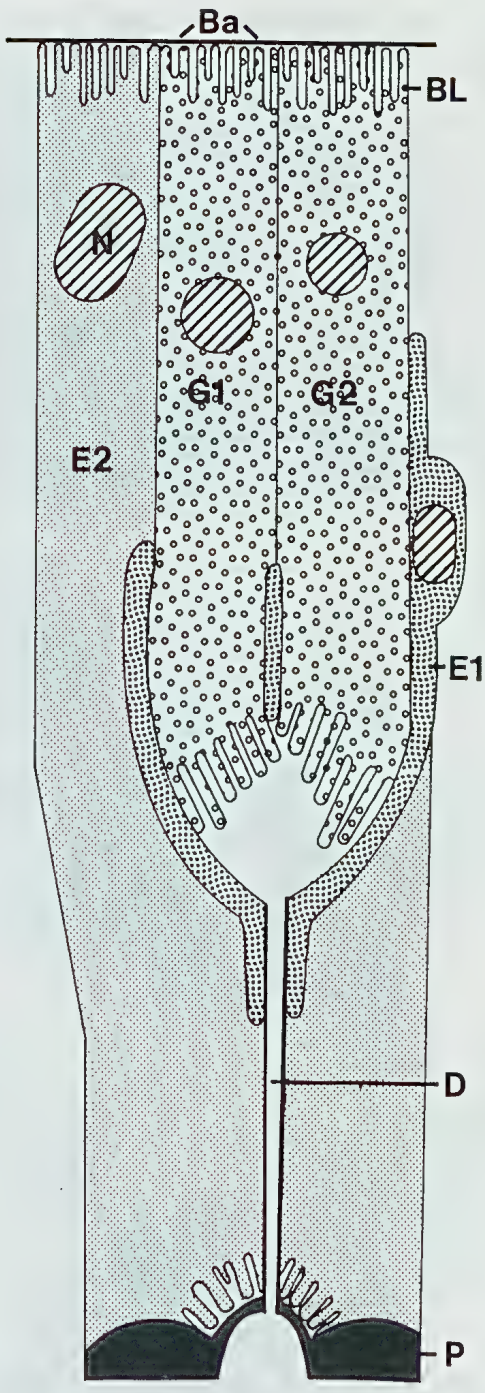
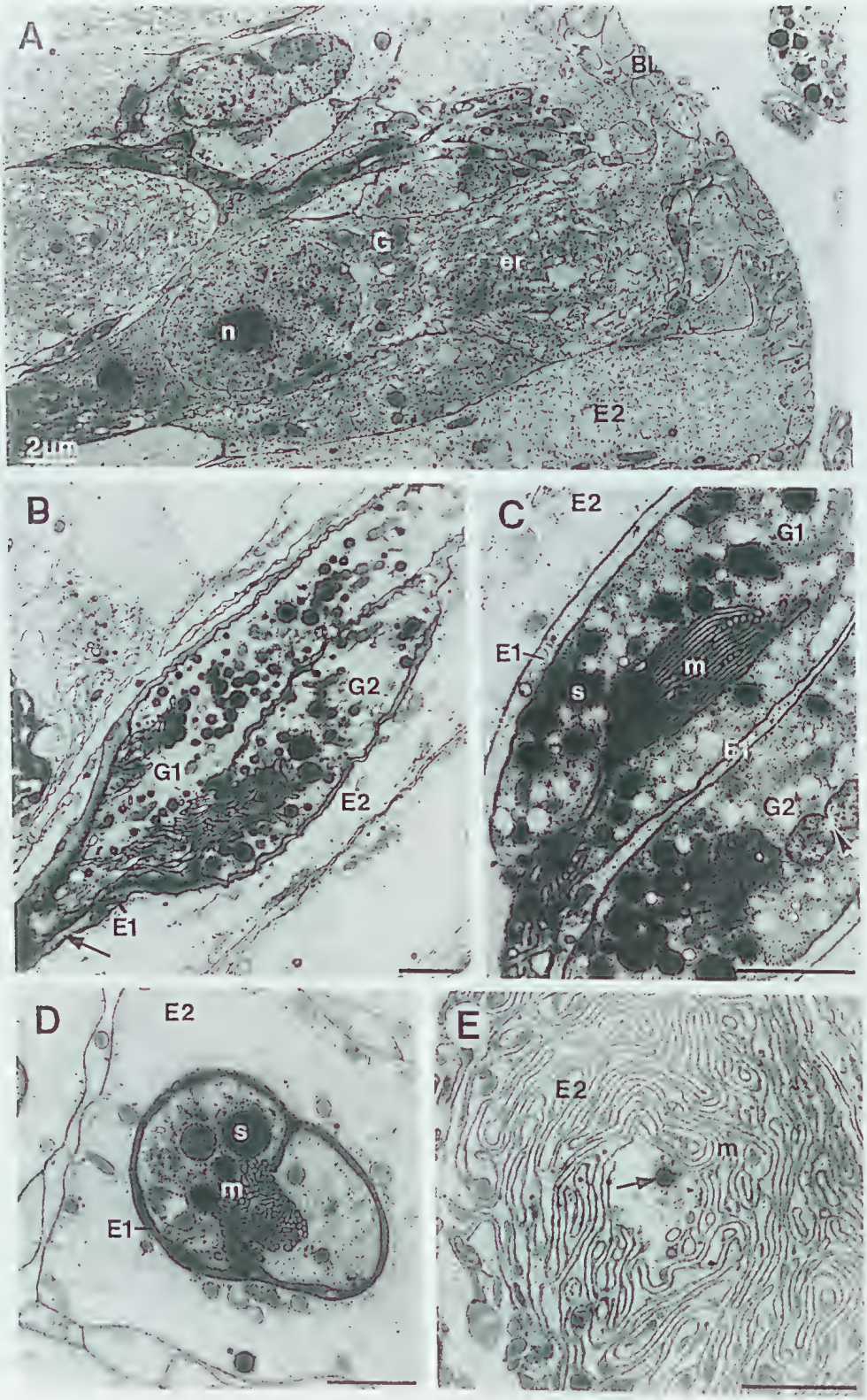


FIG. 4. Schematic reconstruction of one glandular unit of accessory glands. Ba: basal lamina, BL: basal labyrinth, D: ductule, E1: inner envelope cell, E2: outer envelope cell, G1, 2: gland cells, N: nucleus, P: pore plate.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cates that a more complex gland composition as in *P. phalangioides* might not be exceptional.

The glandular units of *P. phalangioides* could function as a two-component-system, as the outer envelope cell shows conspicuous microvilli that surround the orifices of the ductules. This indicates secretory activity although the outer envelope cell contains no stainable secretory droplets or granules. Their product could have got lost during fixation or, the cells produce and release their product only on demand. Not all the secretory activities of cells are accompanied by microscopically detectable accumulation of the product in the cytoplasm. Apart from that, the outer envelope cell exhibits a basal labyrinth. It contributes to enhance the exchange of molecules between the haemolymph and the cells (Berridge and Oschmann, 1972) and characterizes active cells that take up or transfer material from or to the haemolymph.

The glandular secretions might serve various functions such as nutrition of the sperm (Coyle *et al.*, 1983; De Carlo, 1973; Engelhardt, 1910; Forster, 1980), pheromone production (Kovoor, 1981) or sperm displacement from the spermathecae into the genital cavity during oviposition (Forster *et al.*, 1987; Lopez, 1987; Lopez and Juberthie-Jupeau, 1983). Brignoli (1976) and Lopez and Juberthie-Jupeau (1983) considered activation of sperm prior to fertilization. The glandular tissue might be responsible for triggering activation via a secretory product that gets released exclusively before oviposition. Further, the females might achieve advantages from resorbing the sperm mass out of the genital cavity.

I consider the secretion in the female genital tract of *P. phalangioides* serves primarily as a depot for the sperm that guarantees successful storage as the onset of the female receptivity corresponds with the time needed to fill the genital cavity with glandular secretion (Uhl, in press a). Concerning any other possible functions, specific investigations are still lacking.

The bursal storage mode is considered a 'primitive' mode with little survival value as the spermatozoa are liable to be washed out during oviposition (Forster, 1980). Nevertheless, females of *P. phalangioides* succeed in producing several fertile batches of eggs after a single mating (Uhl, in press a).

Although females do not depend on repeated insemination, they allow further copulations. These always last only a few minutes in constrast to the first copulation that lasts over an hour and there is no apparent difference in copulation duration between second copulations with the same or with a different male. If new males are able to replace sperm of a previous male, longer copulations would be expected. Such short copulations may suggest that males are able to assess female virginity or reproductive history during insertion of their palpal structures and then decide on further investment of time and energy.

It has yet to be investigated whether successive copulations result in a transfer of spermatozoa at all, which will also give information on sperm precedence. Provided they transfer sperm and fertilise at least some eggs, it would be advantageous for males to mate with any female they meet. The females, on the other hand, can be expected to fill their storage structure with as many spermatozoa as possible to achieve the highest possible reproductive success. Depending on the amount of sperm already accumulated in the genital cavity females might allow further copulations and hence, decide on copulation duration. Indeed, there is some evidence that the female terminates copulation.

ACKNOWLEDGEMENTS

I wish to thank my supervisor Prof. Dr. P. Weygoldt (Freiburg) for making this work possible. Dr. M. Schmitt (Bonn) and two anonymous referees gave helpful comments on the manuscript. Without a grant from the Studienstiftung des Deutschen Volkes and additional support from the Organizing Committee participation at the XIIth Congress of Arachnology, Brisbane would have been impossible.

FIG. 5. Ultrathin sections of accessory glands. A) Longitudinal section. Nuclear region of gland cells. B, Longitudinal section. Two gland cells join to form common microvilli region, surrounded by two envelope cells forming first part of canal (arrow). C) Longitudinal section. Microvilli region. Arrow shows cleaving bacterium. D) Transversal section. Beginning of ductule. Gland cells joined, enveloped twice. E) Microvilli region of outer envelope cell close to pore plate. Small ductule (arrow); BL: basal labyrinth, E1: Inner envelope cell, E2: outer envelope cell, er: endoplasmatic reticulum, G1: gland cell 1, G2: gland cell 2, n: nucleus, m: microvilli, s: secretory droplets. All scale lines: 2μm.

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THE BIOLOGY OF SPIDERS AND PHENOLOGY OF WANDERING MALES IN A FOREST REMNANT (ARANEAE: MYGALOMORPHAE)

GRAHAM F.C. WISHART

Wishart, G.F.C. 1993 11 11: The biology of spiders and phenology of wandering males in a forest remnant (Araneae: Mygalomorphae). *Memoirs of the Queensland Museum* 33(2): 675-680. Brisbane. ISSN 0079-8835.

Eight syntopic mygalomorph species, four of one genus, are recognised as inhabitants of a small remnant forest. Over six years 1,207 mature males were trapped and collected from a nearby home swimming pool and the wandering times of mature males of the species are compared. The population density within the forest is estimated. It is suggested the high number is because of an 'edge effect' supported by a reduction in predator numbers, an 'island effect' and that mygalomorphs have low dispersion powers, long life cycle and sedentary life style.□*Mygalomorphae, Hadronyche, Misgolas, Stanwellia, community, forest, remnant, phenology, population, syntopic, wandering.*

Graham F.C. Wishart, 'Scalloway', Willowvale, Gerringong, New South Wales 2534, Australia; 23 November, 1992.

Phenological studies of spiders commonly consider the distribution and abundance of species in relation to habitat variation or disturbance (Peck and Whitcomb, 1978; Koch and Majer, 1980). Studies of male spider wandering patterns are less common and are usually associated with taxonomic revisions of particular groups (Coyle, 1971; Raven, 1984). Main (1982) synthesised male wandering data for her studies of arid zone spiders.

This paper presents male wandering patterns over a six year period for six species of syntopic

FIG. 1. Aerial view, easterly aspect, from study site towards Gerringong township.

FIG. 2. Aerial view, south-westerly aspect, of study site. Pool length is 10m.

forest mygalomorphs and also discusses possible ecological effects which could account for the viability of the spider population. The long term data gathering was enabled by the serendipitous location of an in-ground swimming pool acting as a large pit-fall trap close to remnant forest.

STUDY AREA

The study site is on the property 'Scalloway' (34°44'11"S, 150°47'23"E) (Figs. 1, 2), near Gerringong, N.S.W., and is a remnant piece of marginal Complex Notophyll Vine Forest (Bywater, 1978) at an altitude of 110m. It is a fragment (ca 95m x 55m) of the original 'Illawarra Scrub', varying forest types which occupied much of the coastal strip east of the escarpment in South Eastern Australia between the towns of Stanwell Park in the North and Bomaderry on the Shoalhaven River in the south, a distance of 75km. Land clearing removed over 80% of this original vegetation (Fuller and Mills, 1985) and took place mainly between 1850 and 1910, the remnants being restricted to land unsuitable for grazing because of steep gradients and rock outcrops.

The forest overstory includes the trees *Syncarpia glomulifera* and *Alphitonia excelsa* and several vine species forming a discontinuous canopy at a height of about 12m. The understory consists mainly of the small tree *Commersonia fraseri* and the exotic woody scrambling shrub *Lantana camara*. *L. camara* intrudes within the forest but is dense and extensive around the forest edge (not allowed for in the forest dimensions) preventing the entry of cattle.

The site is on the edge of a ridge and slopes rapidly downwards to the north east. The soil is of volcanic origin. The surface soil is thin and spread over a basalt bedrock. Large but moveable rocks are prolific. Leaf litter is ca 5cm deep.

METHODS

Wandering mygalomorph spiders trapped in a 10m long swimming pool 15m from the forest edge were collected daily from 1 July 1985 to 30 June 1991. Variables possibly affecting the numbers of spiders trapped, such as domestic lighting, maintenance of grounds and ability of different species to wander further or more quickly than others, were not taken into account. For three years from 28 August 1986 to 25 October 1989 the burrows within a plot 1.5m^2 were examined weekly.

RESULTS

Community Composition

Mature males of eight species of mygalomorph spiders were collected from the pool, viz.: *Misgolas hubbardi* Wishart, 1992 (Idiopidae), *M. dereki* Wishart, 1992, *M. kirstiae* Wishart, 1992, *M. robertsi* (Main and Mascord, 1974), *Hadronyche* sp. (Illawarra group) and *Atrax* sp.

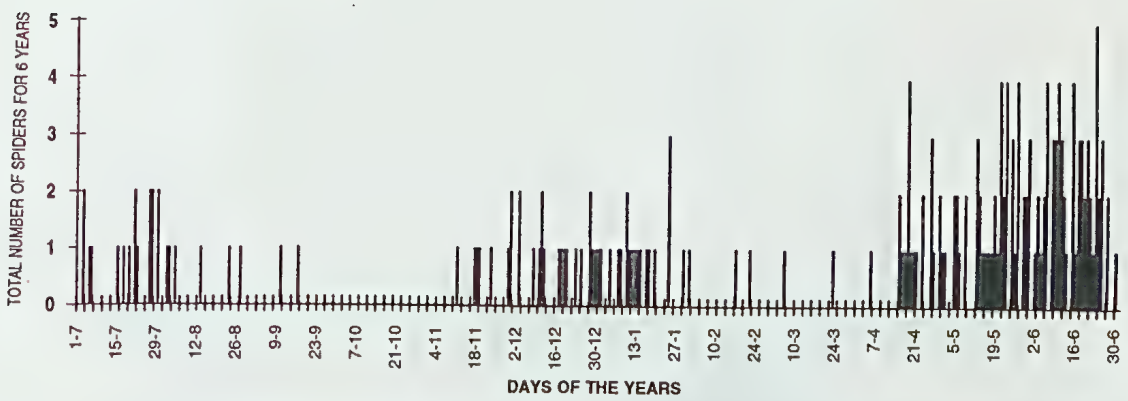

FIG. 3. Total number of *Misgolas hubbardi* captured on same days of years for six years from 1.7.85 to 30.6.91.

(Hexathelidae), *Stanwellia hoggi* (Rainbow, 1914) (Nemesiidae), and *Kiama lachrymoides* Main and Mascord, 1971 (Cyrtaucheniidae). The *Hadronyche* sp. is that referred to as *Hadronyche* sp. 20 by Gray (1987). The *Atrax* sp. is smaller but similar morphologically to *A. robustus* Cambridge, 1877. It differs also in that males wander from October to December whilst those of *A. robustus* wander mainly in January (Gray, 1986). They are considered here to be different species.

Population Density

Because much of the surface area of the forest floor is covered by large rocks and occupied by trees the 1.5 m^2 plot cannot be representative of the whole forest area. However, an extrapolation (based on the assumption that the ratio of the number of burrows occupied by all mature female spider species to the number of burrows occupied by *M. hubbardi* is equivalent to the ratio of the number of captured mature male spiders of all species to the number of captured mature male spiders of *M. hubbardi*) indicates there should be 41 mature female mygalomorphs per m^2 in the 1.5m^2 plot.

In the 1.5m^2 plot the maximum number of burrows counted at one time was 55. These included open burrows, those known to exist but temporarily sealed and very small open burrows of which most failed to persist. There were 27 burrows larger than 8 mm in diameter of which 10 were each occupied by a mature female *M. hubbardi*. Due to physical limitations in accurate-

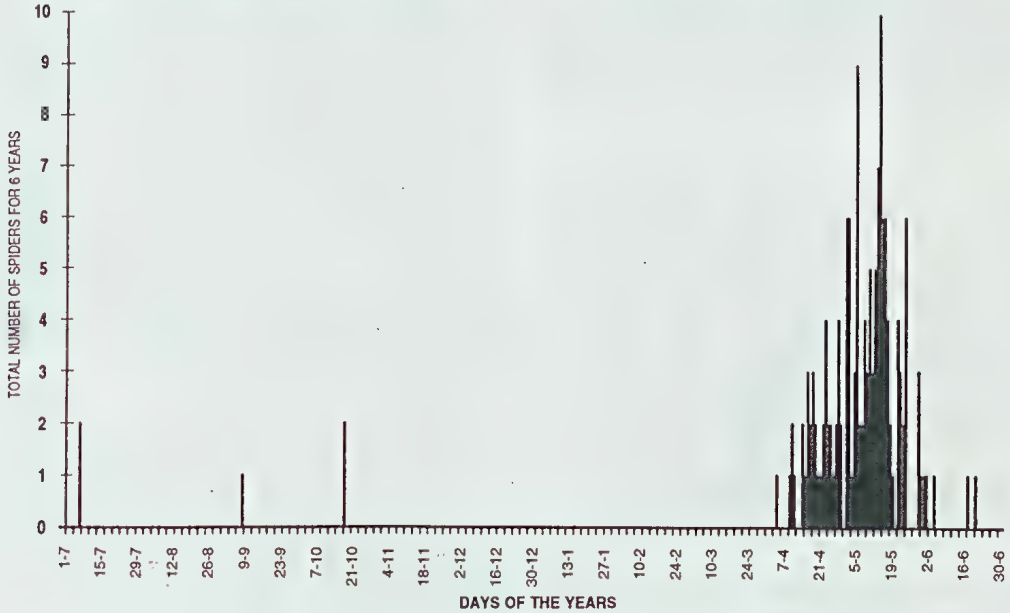

FIG. 4. Total number of *Misgolas dereki* captured on same days of years for six years from 1.7.85 to 30.6.91.

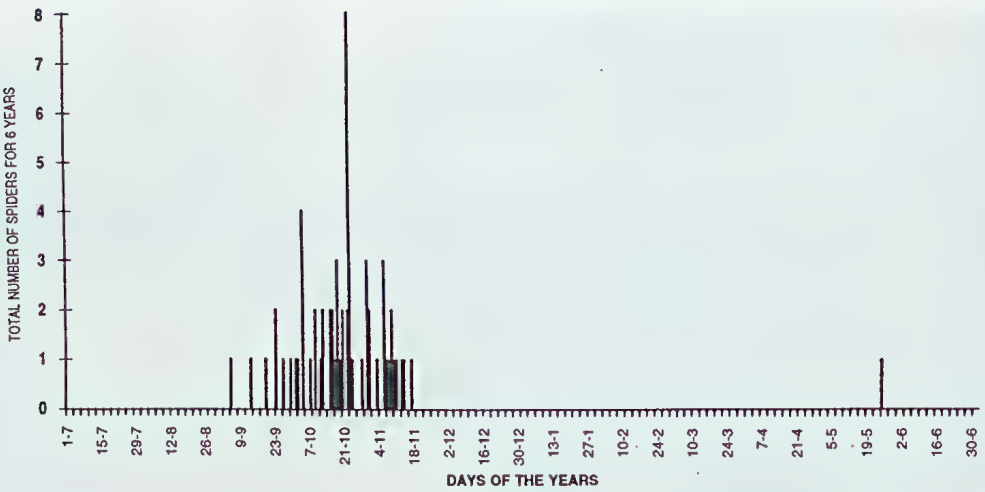

FIG. 5. Total number of *Misgolas kirstiae* captured on same days of years for six years from 1.7.85 to 30.6.91.

ly counting small burrows and recognizing the presence of the burrows of *M. kirstiae* and *Hadronyche* sp. the total count must fall short of the actual mygalomorph population.

PHENOLOGY OF WANDERING MALES (Table 1)

Wandering mature males of *M. hubbardi* were found almost throughout each year (Fig. 3). The extensive wandering period of *M. robertsi* is interrupted during January and February when the frequency of capture is reduced (Fig. 6). The wandering period for *S. hoggi* is also long, extending over six months (Fig. 8). As is customary to expect of male mygalomorphs, the wanderings of *M. dereki* (Fig. 4), *M. kirstiae* (Fig. 5) and *H.* sp. (Fig. 7) are restricted to short and more precise annual periods. The collections of *Atrax* sp. and *K. lachrymoides* were too small for deductions to be conclusive.

During the six year period, 11 female *S. hoggi* were also trapped in the pool during the months from March to October.

Species	Total trapped	Peak active periods	% in peak periods	No. trapped per day
Misgolas hubbardi	197	April-July	58	0-3
		Nov.-Jan.	20	0-2
Misgolas dereki	153	Apr.-June	98	0-7
Misgolas kirstiae	61	Sept.-Nov.	98	0-7
Misgolas robertsi	158	Nov.-May	96	0-4
Hadronyche	606	March-May	96	0-29
Stanwellia hoggi	26	May-Nov.	100	0-1
Atrax sp	5	Oct.-Nov	100	0-2
Kiama lachrymoides	1	Nov		
Total	1207			

TABLE 1. Summary of numbers and timing of male spiders trapped in pool from 1 July 1985 to 30 June 1991.

DISCUSSION

No previous reports have been found of either eight species of mygalomorph spiders or four species of one genus (*Misgolas*) of spiders existing elsewhere syntopically or sympatrically.

The high proportion of mature female *S. hoggi* collected is surprising, 11 females to 26 males, and 10 of the 11 were taken at times coincidental with the male wandering period. The number reflects the long-legged, male-like morphology of the female adapting it to roam. Further, that only one male *K. lachrymoides* was collected may indicate the inability of the male of this species to wander a long distance a reflection in this case of the male's short-legged female-like morphology. The usual sexual dimorphism of mature burrowing mygalomorph spiders (female bulky, stout legged; male less bulky, long legged) is contradicted in these two species.

Some possible reasons for the dense mygalomorph spider population are offered. First, predators of mygalomorph spiders may have become extinct in the area following human settlement. For example, the bandicoot (*Perameles nasuta* Geoffroy, 1804), reputed to be a mygalomorph spider predator (Main, 1976; Preston-Mafham, 1984) and once very common in Willowvale, has been rarely seen by the author and not at all for 15 years. Here then, possibly, is

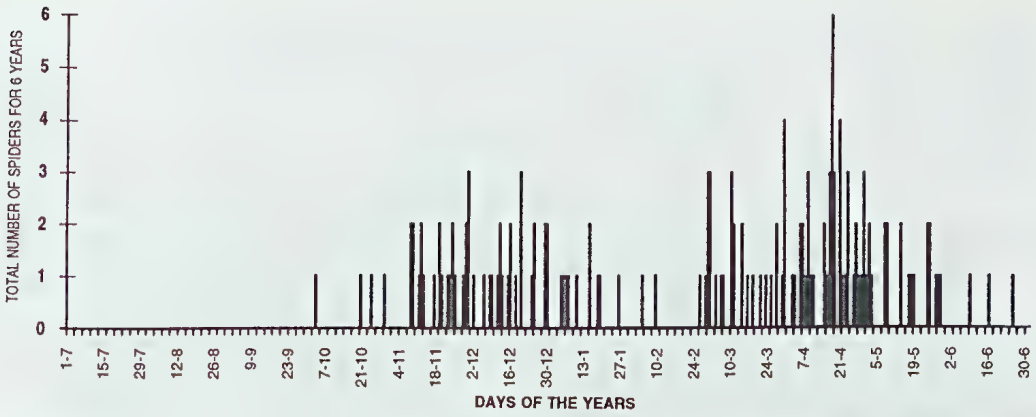

FIG. 6. Total number of *Misgolas robertsi* captured on same days of years for six years from 1.7.85 to 30.6.91.

a paradox where habitat destruction and the introduction of feral animal pests, may increase, not decrease, mygalomorph spider numbers by decreasing spider predators.

Second, the concentration may result from an 'Island Effect' where it is found that the population of an individual species can be far greater than expected when the species is insulated within a small ecological system (separate pers. comms, M.Gray and R.Raven). Also Main (1987) proposed that mygalomorphs are admirably fitted to persist in small isolated areas because of their low dispersion powers, long life cycle and sedentary life style.

Finally, in a larger (ca. 300 ha) forest with complete canopy and separated from the 'Scalloway' site by *ca.* 400m of pasture land there is a paucity of mygalomorph spider burrows and few insects suitable for prey. Burrows are more common near the forest edge, and so too is insect life with grasshoppers, moths and crickets prolific. Because the 'Scalloway' forest remnant is small it is in effect a forest edge throughout with an abundance of suitable prey. Laurence (1991) states, 'In the tropics, forests near edges exhibit striking changes in microclimate, vegetation structure and composition, disturbance regimes, and invasions of species from adjacent habitats. Thus, in fragmented systems, species that tolerate edge conditions are often favoured'. I suggest that this is the explanation for the presence of this dense mygalomorph population.

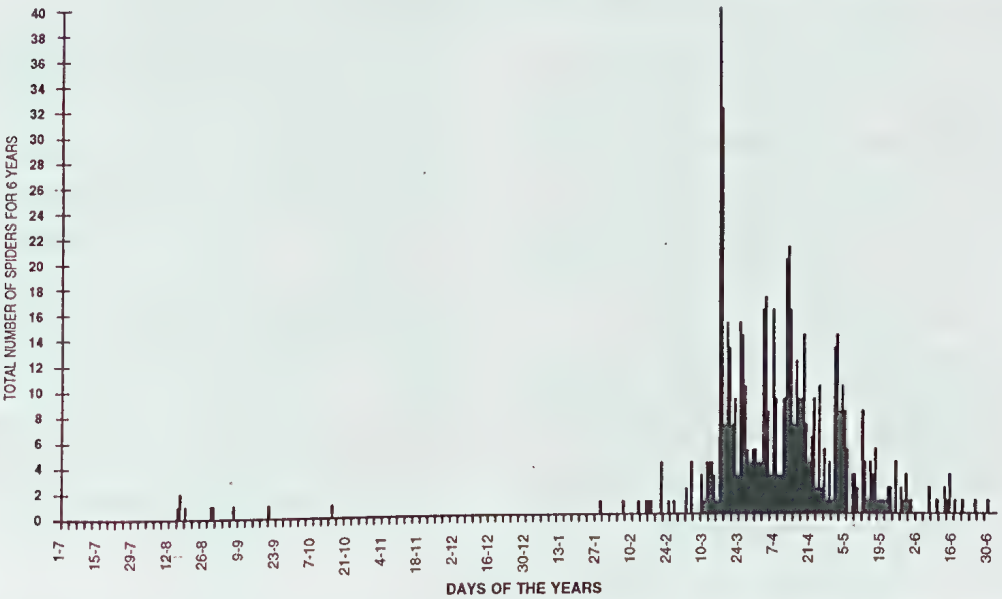

FIG. 7. Total number of *Hadronyche* sp. captured on same days of years for six years from 1.7.85 to 30.6.91.

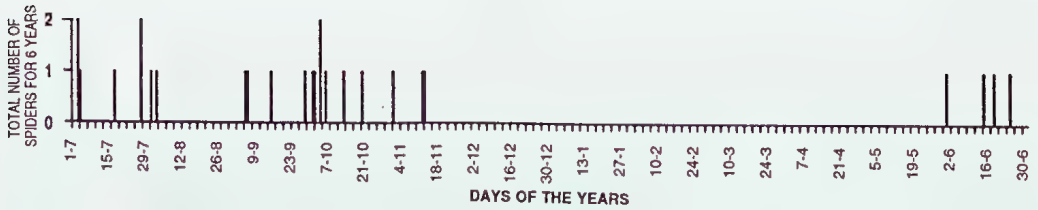

FIG. 8. Total number of *Stanwellia hoggi* captured on same days of years for six years from 1.7.85 to 30.6.91.

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THE MACARONESIAN CAVE-DWELLING SPIDER FAUNA (ARACHNIDA: ARANEAE)

JÖRG WUNDERLICH

Wunderlich, J. 1993 11 11 : The Macaronesian cave-dwelling spider fauna. *Memoirs of the Queensland Museum* 33(2): 681-686. Brisbane. ISSN 0079-8835.

The composition of the cave-dwelling spider fauna of the Macaronesian Islands–Madeira, the Azores and the Canary Islands–is compared with the endemic epigean spider fauna of these archipelagos. The grades of adaptations in the cave-dwelling spiders are compiled, and the following questions are discussed: from which geographic regions did the stem species come? What can be said about the evolution of the species? How old are the cave-dwelling spider species?

Die Fauna der Höhlenspinnen der Makaronesischen Inseln - Madeira, Azoren und Kanarische Inseln- wird mit der endemischen epigäischen Fauna dieser Archipele verglichen. Der Grad der Anpassung an das Höhlenleben wird untersucht und verglichen; die folgenden Fragen werden diskutiert: Wo liegt der Ursprung der Stammarten? Was kann über die Evolution und das Alter der höhlen-bewohnenden Arten gesagt werden?□*Araneae, troglobites, Canarian and Macaronesian Islands, Island biology, biogeography, evolution.*

Jörg Wunderlich, Hindenburgstr. 94, D-75334 Straubenhardt 3, Germany; 7 December, 1992.

Some island groups in the northern Atlantic–the Canary Islands, the Azores, the Archipelago of Madeira, the small Ilhas Selvagens and by most authors (but not by me) the Cape Verde Islands–are called Macaronesian Islands (Fig. 1). The Macaronesian Islands are mainly of volcanic origin, only the Eastern Islands (Fuerteventura, Lanzarote) are partly of continental origin and have been probably connected with Africa some million years ago.

The first troglophilic and troglobitic Macaronesian spiders were described in 1985 from Tenerife. Now cave-dwellers are known from Madeira (1 species), from the Azores (1 species) and from the Canary Islands (at least 17 endemic species, see Wunderlich, 1991), by far most species are known from Tenerife: at least 11 species = 10% of the endemics (and perhaps there are hundreds of mostly undescribed insect species of different orders).

Especially on the Canary Islands there are many caves. The best studied system of caves on Tenerife - cueva del Viento, cueva Reventon - is more than 16km long; the length of all Macaronesian caves is perhaps more than 100km, and only a few have been examined intensively.

MACARONESIAN CAVE-DWELLING SPIDERS

Nearly all cave-dwelling spiders are endemics of one island or even only one cave (Table 1):

Three species of those listed (Table 1) are not restricted to a single island:

1. *Meta bourneti* Simon, 1929 (Tetragnathidae) is a west-palearctic species introduced to a cave on Tenerife (Canary Islands);

2. *Agraecina canariensis* Wunderlich, 1991 (Liocranidae) is known from caves on Gran Canaria and Tenerife (Canary Islands);

3. *Rugathodes pico* (Merrett and Ashmole, 1989) (Theridiidae) is known from caves on Pico and Fajal (Azores).

Here I deal with five questions: 1. What is the composition of the Macaronesian fauna of troglophilic and troglobitic spiders and what are the differences to the epigean fauna? 2. Which species are extremely well adapted as cave-dwellers? 3. From which geographic regions did the stem species come? 4. What can be said about the evolution of the species? 5. How old are the cave-dwelling spider species?

Cave-Dwelling and Epigean Spiders

The most diverse spider families are shown in Figs 2-3. In the Canarian troglophilic and troglobitic cave-dwellers (Fig. 2): Dysderidae (at least 35%), Linyphiidae (25%) and Pholcidae (25%), the sum of these 3 families is 85%. (No Oecobiidae).

In the epigean endemic species (Fig. 3) the composition is quite different: Dysderidae 16%, Linyphiidae 15%, Pholcidae 13%, the sum of these 3 families is 44%, only half compared with the cave-dwellers. In the families Dysderidae

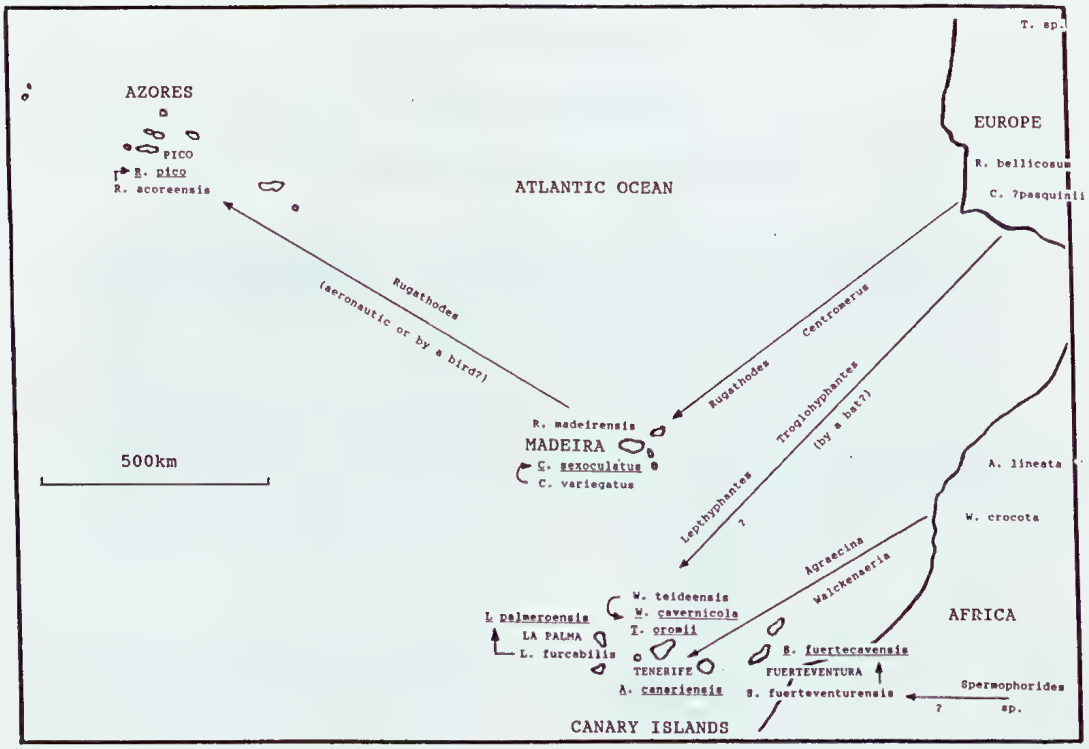


FIG. 1. The Macaronesian Archipelagos. Some Macaronesian cave-dwelling spiders (underlined) and their European and Macaronesian relatives.

(only *Dysdera*) and Pholcidae (*Pholcus* and *Spermophorides*) *all* epigean genera have evolved cave-dwelling species; in the Linyphiidae only members of 5 from 21 genera with endemic species have evolved cave-dwellers (= 25%). *Dysdera* is the genus richest in species in caves and out of caves on the Canarian and Macaronesian Islands. Oecobiidae probably do not find their prey -ants- in the caves.

Highly Adapted Cave-dwellers?

Different grades of adaptation to cave life in the Macaronesian spiders is evident in three structures (Table 1): the size of the eye lenses, the body pigmentation and length and slenderness of legs.

Some true cave spiders of *Dysdera* have reduced eyes, but neither depigmentation nor long and slender legs. I do not know the explanation. Thus, perhaps the eye reduction is the best indicator regarding the grade of adaptation to cave life in spiders. For discussion below I choose the following five spider species.

1. *Meta bourneti* (Tetragnathidae, Tenerife) is restricted to deeper parts of caves, but the eyes are not reduced, the body is only slightly depigmented, and the legs are nearly of normal length. This species has been introduced from Europe or North Africa.

2. Not strongly adapted is *Agraecina canariensis*, but very variable in the depigmentation and in eye reduction (grades 1-3, Figs 4- 5). The variation is intrapopular. This seemingly troglophilic subterranean species is not restricted to caves.

3. In four Canarian species of *Spermophorides*, the eyes are more or less reduced (Figs 8-11); the eyes of an epigean *Spermophorides* sp. from Tenerife are normal (Fig. 12). Cave-dwelling *Spermophorides* spp. are not strongly related. The known species occur on four different islands. So the eye reduction must have been evolved independently four times.

4. *Rugathodes pico* is restricted to caves. The spiders are strongly depigmented, they have strongly reduced eyes and the legs are long and slender (grades 3-4, Fig. 6a; cf. Fig. 6b the related epigean *R. acoreensis*).

5. In *Troglohyphantes oromii* (Ribera and Blasco, 1986) (Linyphiidae, Tenerife), the eyes are tiny or completely absent (Fig. 13), body and legs

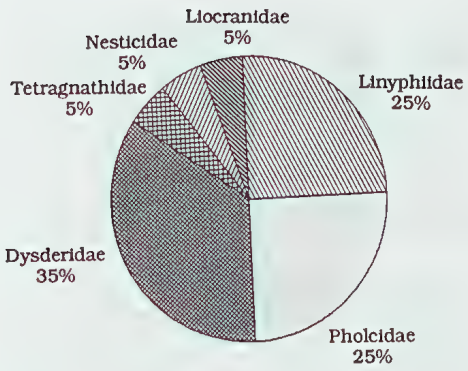


FIG. 2. Composition of Canarian families of troglophilic and troglobitic spiders based on 18 species.

are completely depigmented, the legs are very long and slender (all grades between 3 and 4). The adaptations in *Canarionesticus quadridentatus* (Nesticidae, Tenerife) and in ?*Metopobactrus cavernicola* (Linyphiidae, Tenerife) are similar. These species show the strongest adaptations to cave life.

Origin of the Stem Species

Macaronesian cave-dwelling neoendemic spiders and their European relatives. The hypothetical origin of all species is the West-Mediterranean area, most came from Europe (Fig. 1), e.g. species of *Rugathodes* to the Azores - Madeira seems to be a 'stepping stone', *Centromerus* to Madeira. *Troglohyphantes* came perhaps from Spain to Tenerife, but the sister species is unknown. *Walckenaeria* came from North Africa to Tenerife, *Agraecina* came from

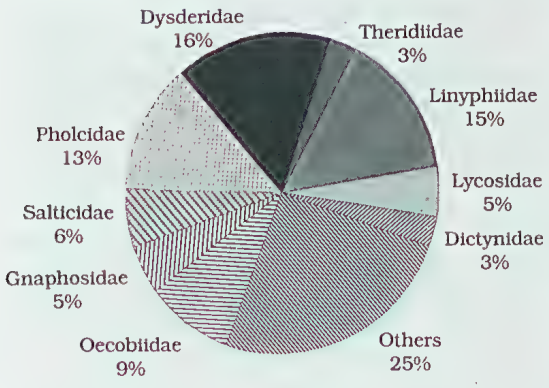


FIG. 3. Composition of Canarian families of *epigean* spiders based on more than 400 species.

Species	Di	R.E.	Dep	Leg	T
Meta bourneti	Wpal,T	0	≤1	≤1	<2
Agraecina canariensis	CI (GC,T)	0-3	0-3	1	1-7
Dysdera labradaensis	CI (T)	2	0	0	2
D. ratonensis	CI (LP)	2	0	0	2
Lepthyphantes palmeroensis	CI (LP)	1	1	1	3
D. chioensis	CI (T)	3	0	1	4
D. ambulotenta	CI (T)	3-4	0	0	3-4
Pholcus baldiosensis	CI (T)	2	3	0	5
Spermophorides flava	CI (GC)	2	3	1	6
S. reventoni	CI (T)	1-2	1	2	≤5
D. esquiveli	CI (T)	?3-4	1	1?	≥5
S. fuerteventurensis	CI (F)	2	3	≤1	≤6
Walckenaeria cavernicola	CI (T)	1-2	1-2	3	6
S. justoi	CI (EH)	2-3	3	3	≤9
D. unguimmanis	CI (T)	4	2-3	≤4	~10
Centromerus sexoculatus	M	3	4	2-3	≤10
Rugathodes pico	AZ	3	3	3-4	≤10
?Metopobactrus cavernicola	CI (T)	3-4	3	3-4	~10
Troglohyphantes oromii	CI (T)	3-4	4	3-4	~11
Canarionesticus quadridentatus	CI (T)	4	3	4	11

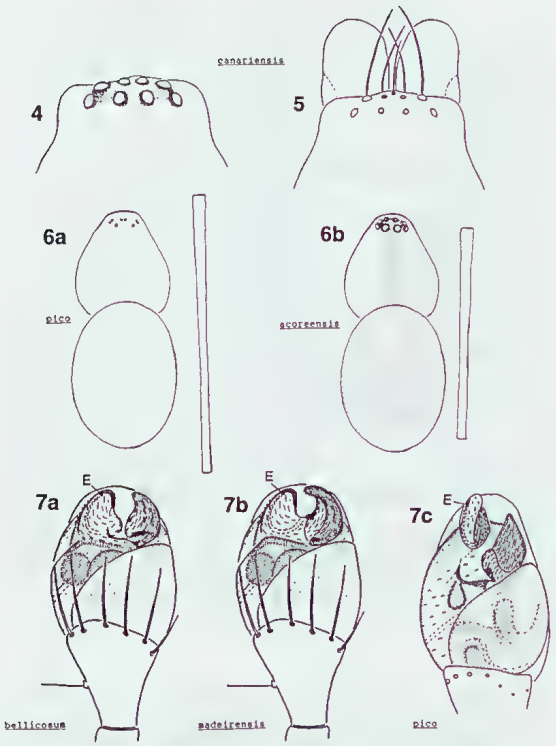
TABLE 1. The Macaronesian troglophilic (at least the first two and perhaps the first five species) and troglobitic spider species and the grades of their adaptations from 0 (normal structures as in epigean taxa) to 4 (=eyeless or almost so/ completely depigmented/ very long legs, the species listed below); AZ = Azores, CI = Canary Islands, EH = El Hierro, F = Fuerteventura, GC = Gran Canaria, LP = La Palma, M = Madeira, T = Tenerife, Wpal = West Palearctic). Di, distribution; R.E., reduced eyes, Dep, depigmentation; Leg, long & slender legs; T, Total.

Europe or North Africa to Tenerife (and Gran Canaria).

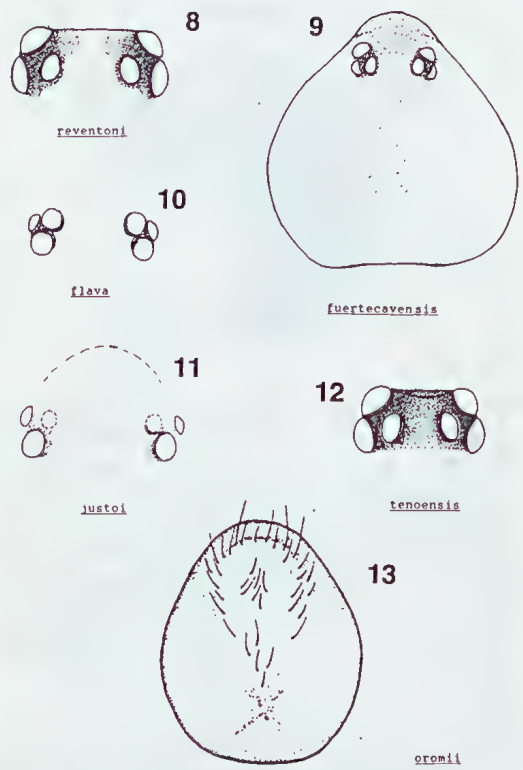
The occurrence of cave-dwelling species of the different genera on *Tenerife* - e.g. *Walckenaeria*, *Troglohyphantes* and *Agraecina* - are remarkable (Fig. 1). The highest Macaronesian mountain, the 3718m high Teide on Tenerife, seems to be a 'catcher' of aeronautic (ballooning) spiders which came from the Western Mediterranean area. This finding is supported by the relationships of the endemic spider fauna of the Teide and the Cañadas, an area surrounding this high mountain (cf. Wunderlich, 1991: 104-107).

Evolution of Macaronesian Cave-dwelling Spiders

In some spiders, e.g. *Canarionesticus quadridentatus* and *Troglohyphantes oromii*, no related epigean species is known, and almost nothing can be concluded about their evolution.



FIGS 4-7. 4-5. Variable eye reduction in subterranean Canarian *Agraecina canariensis* Wunderlich, 1991 (Liocranidae). 6, 7. *Rugathodes*. 6, ♂ body with eyes and right tibia I from the Azores: 6a, of the cave-dwelling *R. pico*; 6b, of the epigean *R. acoreensis*. 7. Right male pedipalps ventral: 7a, *R. bellicosum* (Simon, 1873), Europe; 7b, *R. madeirensis* Wunderlich, 1987, Madeira; 7c, *R. pico* (cavernicolous) and *R. acoreensis* (epigean), Azores. These species show no differences. (E = embolus).



FIGS 8-11. Eye reduction in Canarian cave-dwellers spiders: 8, *Spermophorides reventoni* Wunderlich, 1991; Fig. 9, *S. fuertecavensis*; 10, *S. flava* Wunderlich, 1991; 11, *S. justoi* Wunderlich, 1991. 12. Eyes of the epigean *S. tenoensis* Wunderlich, 1991, Tenerife. 13. Sometimes completely eyeless prosoma of cave-dwelling *Troglohyphantes oromii*, Tenerife.

(Several species are not well studied, e.g. *Dysdera* species, or only one sex is known). In this connection *Troglohyphantes oromii* is of special interest because nearly all species of this genus are troglophilic or troglobitic cave-dwellers as well as the species from Tenerife. I can imagine that there has never existed an epigean stem species on Tenerife and that the ancestors, perhaps as a cocoon, has been transported by a bat directly from a European cave to a cave on Tenerife. Several species or subspecies of bats fly from Europe via Madeira to the Canary Islands (Dr. Biscoito, Mus. Munic. Funchal, Madeira, pers. comm.). This hypothesis would explain why there is no epigean *Troglohyphantes* spp. on Tenerife or another Canary or Macaronesian Island. Otherwise I do not want to exclude the possibility that this species is a paleoendemic relict (Peck, 1990: 372-373).

Based on the very similar genital organ, in *Rugathodes pico* and *acoreensis* they are identical, I found some strongly related spider species (Table 3). In the cave-dwelling *R. pico* (Table 1 and discussed above), the adaptations to cave life and the differences in some non-genital structures compared with epigean species are very distinct: the eye reduction, the depigmentation and the prolongation of the legs, Fig. 6a; compare Fig. 6b of the epigean species, which is also known from the Azores. Otherwise the genital structures in the two Azorean species show *no* differences in both sexes (Fig. 7c), but there are distinct differences to *madeirensis* from Madeira (Fig. 7b) and *bellicosum* from Europe (Fig. 7a). So I do believe that *R. pico* and *R. acoreensis* are true sibling

Introduced species	Paleaoendemic species	Neoendemics
Meta bourneti	*Canarionesticus quadridentatus* (Nesticidae, Tenerife). No known relative.	The epigean sibling or sister species/stem species is known, usually from same island. To this group belong most Macaronesian cave spiders, see below (genesis/evolution), Dysderidae, Pholcidae, Linyphiidae, Theridiidae and Liocranidae.

TABLE 2. Historical groups of Macaronesian cave-dwelling spiders. Position of *Troglohyphantes oromii* in list is uncertain; it has no known epigean relative. See below: possible transport by a bat.

species (or even subspecies?) and that *R. acoreensis* also is the stem species of *R. pico*.

In *Spermophorides*, differences in genital and non-genital structures are distinct in both sexes, and perhaps they are not sister species. The remaining species in this list are known only from females.

Martin *et al.* (1989) assume that some Canarian troglobites can be considered as relict species which evolved after changes in the climate 'since there have been alternating wet and dry periods ... causing important changes in the fragile insular ecosystem on the surface.' (See below: *Rugathodes*). Furthermore the yearly seasonal changes–hot and dry summers, cooler and more humid winters especially on the Eastern Canary Islands–did perhaps initiate vertical movement of some species into the ground in the summer and also autecological changes for instance in *Centromerus fuerteventurensis* Wunderlich, 1991 (Linyphiidae). In this species, which is not a cave-dweller, the eyes are reduced as well as in species of *Scotargus* (Linyphiidae) and *Altella* (Dictynidae) of other Canarian islands (Wunderlich, 1991).

Borges and Oromi (1991) do prefer the 'adaptive shifting theory' of Howarth (1973). 'This theory does not invoke isolation during climatic (or volcanic?) changes but instead proposes that the partly adapted ancestors shifted into newly developed niches.' In my opinion this theory can well explain the genesis of some Macaronesian cave-dwelling spider species including the ones listed above (see Peck, 1990: 366-368). Especially there exists large caves and lava tubes on the Canary Islands, and there are many ecological niches.

From the Macaronesian Islands and its spiders I know three kinds of preadaptations which support the 'adaptive shifting theory':

1. A lot of Canarian species are known as hypogean spiders and were caught using special traps in the ground in the so-called 'mesocavernous shallow stratum' (Wunderlich, 1991: 11). From this stratum and from accidental captures under stones I know Canarian species of *Dysdera*, *Spermophorides*, *Lepthyphantes*, *Walckenaeria*, *Altella*, *Zimirina* and others. These spiders have moderately reduced eyes and are more or less depigmented, they seem to be troglophilous and not macrocavernicolous, but microcavernicolous or myrmecophilous. *Agraecina canariensis* is a species of this stratum but it also penetrates caves. (A closely related species has been newly discovered in a Romanian cave).

2. Another preadaptation is offered in the conditions in the laurisilva (the relict laurel forest): high humidity and low changes in temperature. For example I found the laurisilva species *Troglonata madeirensis* Wunderlich, 1987 (Anapidae s.l.) in the wet and light part near the entrance of a cave on Madeira (Sao Vincente). I collected ♂ ♀ of *Lepthyphantes mauli* Wunderlich, 1991 (Linyphiidae) in the same part of this cave; this species probably also came from the wet forest near the cave.

3. The third kind of biotopes that lead to troglobitic conditions are under stones and under leaves on trees at places with a high humidity near stretches of water. At such places, under stones as well as under leaves on trees, I found on the Azores *R. acoreensis*, the epigean sibling/stem species of the cave-dwelling *R. pico*. Under a stone over flowing water on Tenerife I found partly depigmented spiders of *Walckenaeria alba*.

Age of Macaronesian Cave-dwelling Spider Species

The age of the Macaronesian caves remains unknown. The youngest Macaronesian Islands, the Western Azorean and the Western Canarian Islands, are only very few (1-2?) million years old. Two spider species, *Pholcus roquensis* and *Walckenaeria cavernicola*, are cave-dwellers at the Cañadas on Tenerife. The greatest age of these species could be the same as the age of this part of Tenerife, at least 200 000 (up to 2 million) years.

Rugathodes pico is known only from caves of the Azorean islands Pico (a young island) and Fajal. After Ashmole (in litt. 1991) these Azorean

Cave-dwelling species	Epigean relatives	Island	Family
Spermophorides fuertecavensis	*S. ?fuerteventurensis*	Fuerteventura (Canary Is.)	Pholcidae
Centromerus sexoculatus, and sp. nov.	*C. variegatus*	Madeira	Linyphiidae
Lepthyphantes palmeroensis	*L.furcabilis*	La Palma (Canary Is.)	Linyphiidae
Walckenaeria cavernicola	*W.teideensis*	Tenerife (Canary Is.)	Linyphiidae
Rugathodes pico	*R.acoreensisi*	Pico and Fajal (Azores)	Theridiidae

TABLE 3. Macaronesian cave-dwelling troglophilic or troglobitic spiders and their nearest epigean relatives, possible stem/ sister/sibling species from same island.

Islands had perhaps a land bridge during the last glaciation. So this species probably evolved from its closely related epigean stem species, near or identical with *R. acoreensis*, perhaps not later than 10 000 years ago (= 10 000 generations). From genital structures, in both sexes there are no differences, speciation should have happened, geologically, not long ago, that means at the end of the last glaciation. But this idea is very vague; perhaps the speciation happened much later, and *R. pico* was transported by bats from one island to the other only very few thousand years ago (Wunderlich, 1991: 200-201). Wunderlich (1991) gives further details of these cave-dwelling spiders and their taxonomy.

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RELATIONSHIP BETWEEN FOOD INTAKE AND SPIDER SIZE IN TEMPERATE ZONES: EXPERIMENTAL MODEL FOR AN ORB-WEAVING SPIDER

FRÉDÉRIC YSNEL

Ysnel, F. 1993 11 11: Relationship between food intake and spider size in temperate zones: experimental model for an orb-weaving spider. *Memoirs of the Queensland Museum* **33**(2): 687-692. Brisbane. ISSN 0079-8835.

A method is presented that allows calculation of the energy intake by an orb-weaving spider, *Larinioides cornutus* (Araneae: Araneidae) under natural conditions throughout the spider's life. A laboratory study provides several relationships between individual energetic consumption and size of spiders depending on the thermal conditions of their environment. I observe a preferred temperature (21°C) at which spiders have the biggest consumption. A model (pseudo-cubic spline) is constructed for the calculation of energy intake by each juvenile instar. Energy requirements of the adult population are estimated from the reproduction rate observed in the field. The energy requirements under natural conditions and the total weight of prey consumed by the population in the course of its biological cycle can be inferred. In the mesophilous heathland investigated, the total fresh weight of prey consumed by the population during the life cycle is 18.2 $kg.ha^{-1}$.

Cette étude vise à relier les taux de survie, de croissance et de reproduction d une espèce Orbitèle *Larinioides cornutus* (Araneae: Araneidae), au nombre de proies consommées en milieu naturel au cours du cycle biologique. Cette analyse est déduite d une approche bioénergétique. Au laboratoire, les consommations énergétiques et la croissance des araignées sont testées en fonction de l environnement thermique. Ces expériences mettent en évidence la présence d un optimum thermique d ingestion qui modifie la croissance et la consommation des individus. Un modèle d ajustement (spline pseudo-cubique) liant la température, la taille des araignées et la température ambiante est proposé pour estimer l énergie ingérée en phase juvénile. L énergie ingérée en phase adulte est estimée en comparant les paramètres taux de reproduction -consommation calculés en élevage, au taux de reproduction observés en milieu naturel. Les besoins énergétiques sont ensuite convertis en quantité de proies capturées. Sur la lande mésophile étudiée, la population capture en poids frais, 18.2 kg de proies par hectare au cours du cycle biologique.□*Population energetics, Araneae, Araneidae, Larinioides cornutus.*

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Among the many studies already carried out about the trophic spectrum of the araneids (Nentwig, 1987), some suggest that the population of spiders–wandering spiders or non-migrant spiders–can utilize a significant proportion of the secondary productivity of natural areas (Kajak, 1967; Robinson and Robinson 1970; van Hook, 1971; Blandin and Celerier, 1981; Nyffeler, 1982). Moreover, some studies emphasize that the growth increment (Vollrath, 1988), the rate of reproduction (Riechert, 1974; Wise, 1979) or the density of individuals (Kajak, 1977) observed in the populations can fluctuate with the number of prey caught. Thus, the characteristics of population dynamics of spiders partly depend on the quantity of prey captured; they can give data about the secondary productivity and consequently about the biological resources of natural biotopes.

However, no study has been done in temperate climates to link the characteristics of population dynamics of spiders with the quantity or the quality of trophic resources. My work on *Larinioides cornutus* (Clerk, 1758) (Araneae: Araneidae) (Ysnel, 1989) describes demographic evolution and reproduction rate of a population in a mesophilous heathland in western France (Ysnel, in press). Besides this, laboratory studies showed a thermal dependance between spider size and food intake (Ysnel, 1990). This study attempts to combine previous results to estimate the number of prey captured by a natural population of spiders during its development.

MATERIALS AND METHODS

This study is based on the calculation of the energy intake during the postembryonic develop-

Instar	13°C		16.5°C		21°C		26°C	
	n	C ±SD	n	C ±SD	n	C ±SD	n	C ±SD
J2	-	-	7	19.03 (5.03)	8	18.75 (6.38	7	12.70 (3.3)
J3	-	-	7	44.60 (11.25)	8	50.54 (24.39)	7	28.74 (13.97)
J4	-	-	9	116.70 (26.9)	14	83.88 (37.86)	12	74.90 (37.8)
J5	2	165	9	241.62 (71.75)	13	134.00 (32.5)	9	181.66 (111.9)
J6	-	-	7	471.95 (190.12)	12	333.90 (86.27)	9	595 (196.56)
J7	6	1438.4 (393)	7	999.14 (317.15)	12	647.70 (166.65)	3	668.39 (22.55)
J8	-	-	-	-	4	1120.69 (456)	1	2581.5
J9	-	-	-	-	1	1029.6	-	-

TABLE 1: Average values of consumption (C, joules) during each juvenile instar. (n = number of individuals tested, SD = standard deviation).

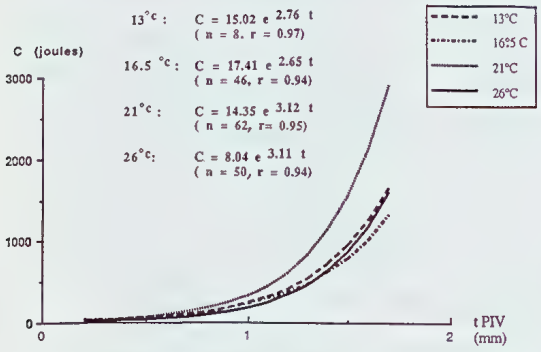

FIG. 1. Theoretical relationship between spider size and consumption in intermoult periods (n = no. of measurements, r = correlation coefficient).

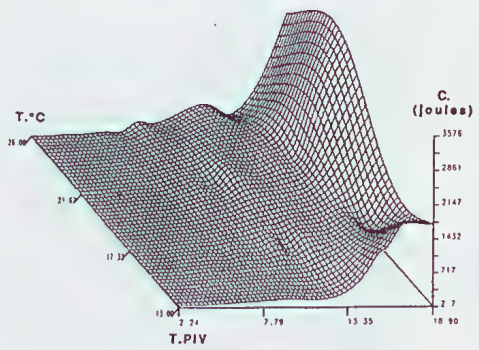

FIG. 2. Pseudo-cubic spline showing relationship between spider size (T PIV), consumption in intermoult period (C) and air temperature (T°C).

ment of *L. cornutus*. To estimate energy requirements during juvenile development, I refer to results on the individual energy consumption of spiders at different temperatures (Ysnel, 1990); thus, only the main references of the experimental conditions are described. Young spiders from cocoons reared in the laboratory were divided into three groups by temperatures-16.5°C, 21°C and 26°C. (These values are a little lower than those in my previous work; they agree with more accurate values using an electronic thermograph). Spiders required a varied diet for survival therefore they were reared to maturity using three prey species: the first instars were fed with adult *Drosophila melanogaster* and the last instars were fed with calliphorid flies (*Calliphora vomitaria* and *Lucilia sericata*). Three times a week, all spiders received a fixed number of prey according to their age. Juvenile spiders were kept under a light regime of LD 12:12. Furthermore, 8 spiders collected in the field at stages 4 and 6 and were reared in the laboratory at 13°C. For these spiders, the energy consumption was studied after the first moult in captivity.

As adults, only females feed (adult males no longer build webs). In nature, females can mate in autumn but egg-laying occurs only under long days from May to August. During this period, females lay, on average, only one egg-sac and disappear soon after laying (Ysnel, in press). Therefore, energy consumption is estimated in

Instar	13°C		16.5°C		21°C		26°C		
		T±SD	n	T±SD	n	T±SD	n	T±SD	K.W.
J2	-	-	7	0.27±0.033	8	0.28±0.024	7	0.27±0.026	P<0.7
J3	-	-	7	0.40±0.043	9	0.37±0.018	8	0.37±0.032	P<0.2
J4	-	-	6	0.56±0.07	12	0.47±0.05	9	0.58±0.09	P<0.05
J5	2	0.87	9	0.91±0.142	13	0.64±0.08	10	0.86±0.13	P<0.08
J6	-	-	6	1.24±0.186	10	0.92±0.105	9	1.42±0.27	P<0.08
J7	6	1.68±0.1	7	1.63±0.237	11	1.21±0.143	3	1.34±0.04	P<0.04
J8	-	-	-	-	4	1.49±0.11	1	1.89	-
J9	-	-	-	-	1	1.66	-	-	-

TABLE 2. Average lengths of tibia IV (T, mm) and comparison of values for 16.5°C, 21°C and 26°C. (n = no. of measurements, SD = standard deviation K.W. = Kruskall- Wallis test).

13°C				16.5°C				21°C			
T	N1	C	C/egg	T	N1	C	C/egg	T	N1	C	C/egg
2.25	115	1083.15	9.41	2.15	82	772.85	9.425	2.13	78	797.1	10.2
2.32	131	1215.20	9.27	2.40	95	679.20	7.14	2.10	87	719.3	8.26
2.50	144	1333.00	9.25	2.28	96	700.40	7.30	2.40	140	1338.9	9.50
2.02	108	948.70	8.77	2.13	50	569.13	11.38	1.87	40	600.71	2.01
2.03	105	-		2.10	75	-		1.80	50	644.31	2.90
2.47	128	-		2.24	65	-		2.02	57	723.81	0.05
2.45	138	-						1.98	58	871.8	15.03
2.43	126	-	-								

TABLE 3. Consumption of ♀ and no. of eggs /cocoons at 3 temperatures. (T = length of tibia 4 ; N1 = no. eggs/first egg-sac; C=energy intake by / in joules; C/egg =energy intake for pro-duction of 1 egg).

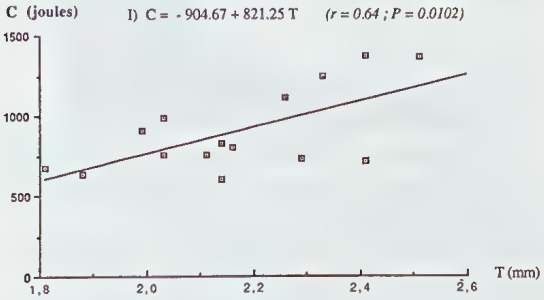

FIG. 3. Relationship between size of females (T) and energy (C) required to elaborate first egg-sac.

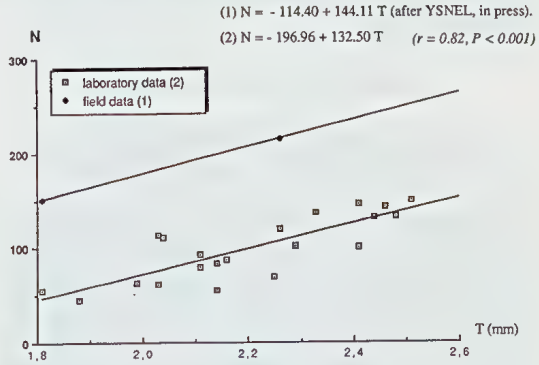

FIG. 4. Relationship between no.of eggs (N) produced in first cocoon and size (T) of females.

adults based on the energy intake needed to produce one cocoon. With this aim, 22 over-wintering fecund females were collected and reared in the laboratory under long days (LD = 16 : 8) and different temperature conditions (13°C, 16.5°C, and 21°C). After the females oviposited, we determined the relationship between the energy intake, the female size (length of tibia IV) and the number of eggs per cocoon.

For each juvenile instar and the adult, the energy intake was determined by the difference between the energy in the whole captured prey and that in the food remains. Calorific determinations for all prey and food remains were made using a Parr bomb calorimeter (Ysnel, 1990).

From the phenology of different instars in nature, the developments of the species have been worked out (Ysnel, in press). Spiderlings emerging from egg sacs laid from late spring to early summer become adult before winter and form a first cohort of individuals (cohort C1). Spiderlings which appear later (end of summer) form a second cohort in the population (cohort C2); they are still immature in winter and become adults early next summer. In analysing the demographic evolution of the population (from 20 m^2 sample areas) during the life cycle, the number of surviving spiders per instar was counted for the two cohorts (Ysnel, 1992). For each juvenile instar, the energy consumption was inferred from the average size of spiders (length of tibia IV) and the thermal environment in the field. Daily meteorological data were classified in four temperature classes (T< 16°C; 16.5°C <T< 18°C; 18.5°C < T < 22°C; T > 22°C) and the average value of each class calculated. The energy ingested is determined from the relative proportion of each phase of temperature during one intermoult period. The average value of the caloric

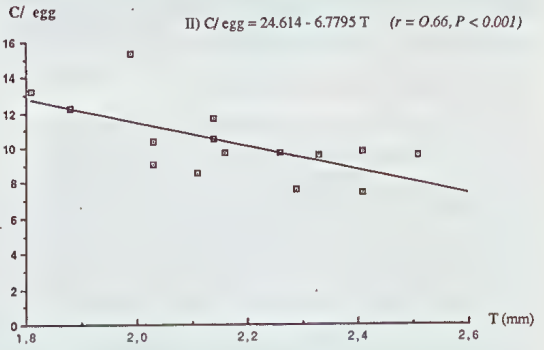

FIG. 5. Relationship between energy required to produce one egg (C/egg/Joules) and size of ♀ (T).

Method 1				Method 2				
Size	TNEL	C(J) (lab.)	TNEF	C (J) (field)	Size	TNEF	C/egg (J)	C (J) Field
2	68.4	737.83	173.8	1874. 8	2	173.8	11.05	1921.4
2.3	107.8	984.2	217.0	1981.6	2.3	217.0	9.02	1957.8
2.6	147.5	1230.6	260.9	2176.4	2.6	260.9	8.30	2165.1

TABLE 4. Comparison of consumption (C, joules) of adult ♀ from methods 1, 2. Theoretical no. of eggs (laboratory, TNEL), in (field, TNEF).

equivalent of insects captured in the field is 22.6 J/mg dry weight (Ysnel, 1992). Cummins and Wuyscheck (1971) found that the dry weight of most insects is equivalent to 20-30% of the wet weight. To transform dry weight (x) into wet weight (Y), I used the conversion factor calculated for calliphorid flies (Y = x/0.262; Ysnel, 1990).

RESULTS AND DISCUSSION

Individual Consumption, Spider Size and Thermal Conditions of Juveniles

The number of instars needed to reach maturity varied with the growth conditions. In Araneidae, the first free-living instar is called J2 (Canard, 1987). From 5 to 8 immature instars may variously precede adulthood. Average consumptions per instar are calculated for four temperatures (Table 1). Average consumption also varies with instar and growth conditions. In each group, an overall connection between the instar of development of a spider and the energy intake of that instar cannot be deduced because individual variation is considerable. However, for all individuals, whatever the instar, there is a good correlation between individual consumption and spider size the intermoult (Table 2). For each temperature with all instars merged, we can fit all the observed values to four exponential graphs corresponding to four different equations (Fig. 1). The four curves show that the individual consumption varies with temperature. For the tested temperature range, and spiders of similar size, I observed a 'preferred temperature of consumption' (21°C) at which the energy intake at the intermoult is maximal (Ysnel, 1990).

Near the thermal preferendum, spiders have the highest consumption but the growth increment is paradoxically the smallest. From instars J4 onwards, individuals kept at 21°C are significantly smaller in size than individuals kept at 16.5°C and 26°C (Kruskall-Wallis test, Table 2). Using the energy budget equation of Petrusewicz and MacFadyen (1970), the energy dissipated as heat (respiration) could be increasing (while the energy retained as growth is decreasing) and the spiders must be more active at 21°C. In contrast, when the temperature deviates from the thermal preferendum, the energy allowed for the activity of spiders must be less important (probably because spiders progressively fall into quiescence or aestivation) and the energy retained as growth increases.

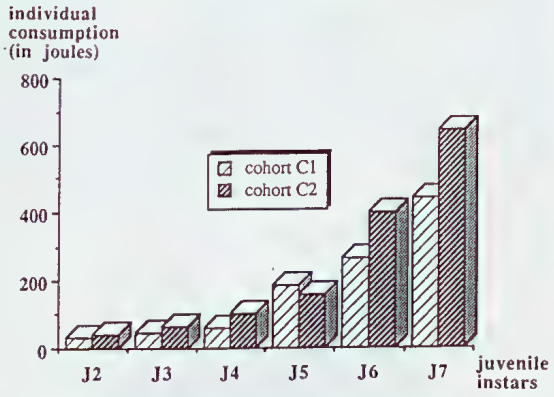

FIG. 6. Estimated individual consumption per instar under field conditions.

One can estimate the energetic requirements of spiders C (ρ)(x, y), by interpolating the pooled data to a single regression model linking spider size and air temperature during the intermoult, to the individual energy consumption. The method, based on the 'homogeneous spline functions with several variables' (Duchon, 1980) allows us to

	Cohort C1				Cohort C2				Population		
Instar	Size	C ind.	n	C1	Size	C ind.	n	C2	N/m^2	C	kg/ha
J2	0.260	30.5	247	7528	0.26	44	159	6996	20.3	14254	1.22
J3	0.363	45.8	127	5817	0.40	63.38	92	5831	11	11648	0.98
J4	0.558	60.9	102	6212	0.57	101.8	29	2952	6.6	9164	0.77
J5	0.831	187.7	86.5	16240	0.78	158	28	4424	5.7	20664	1.74
J6	1.140	264.8	71	18801	1.14	400.54	27	10815	4.9	29216	2.50
J7	1.330	442.3	18	7961	1.36	641.8	7	4493	1.25	12454	1.05

TABLE 5. Estimated mean energy consumption per juvenile instar in field conditions of individuals (C.ind.), all Cohorts 1 (C1) & 2 (C2), & of total population (C); n =abundance of different instars; N/m^2= spider density; kg/ha =mean total weight (kg/ha) of food consumed/instar).(Ysnel, 1992).

	size ± SD	N	C/egg	E/Fn	C	
Cohort C1	1.945 ± 0.18	169	11.43	1931.7	24	46361
Cohort C2	1.91 ± 0.13	164	11.66	1912.2	37	70751

TABLE 6. Estimated mean energy consumption of adults (N = estimated no. of eggs/cocoon; E/egg = energy intake to produce one egg; E/F = energy intake by ♀; n: = no. ♀ ♀ per cohort; C = total consumption of ♀ ♀/ cohort).

adjust significantly the whole experimental values to a pseudo-cubic spline (Fig. 2) by means of the following formula :

$$C(\rho)(x,y)=\sum_{i=1}^{n} \lambda i \, (\rho)((x-xi)^2+(y-yi)^2)^{\frac{3}{2}}+\alpha 1x+\alpha 2y+\beta$$

where ρ is the tension parameter ($\rho = 5$), x = spider size at intermoult, y = air temperature. αi, $\alpha 1$, $\alpha 2$ and β are calculated by the solution of a linear system.

This model estimates the energy requirements during an intermoult period of any juvenile instar, under these experimental conditions.

Energy Consumption during Adult Phase

The individual consumption of all females (Table 3) is plotted against spider size (Fig. 3); the regression line can be used as a calibration curve to estimate the consumption of females independent of thermal environment. The number of eggs per cocoon also showed a significant linear relationship (Fig. 4) with female size.

However, the number of eggs in cocoons in the laboratory (line 2) and those in nature (line 1) clearly indicate that breeding females produce fewer eggs in the laboratory. Two hypotheses can be advanced to explain this result:

- the food consumption of breeding females in the laboratory is lower than that of females in nature; consequently fewer eggs are produced in the laboratory.
- for females of the same size, the number of eggs produced in nature is favoured by a varied diet.

The ratio 'energy consumption/number of eggs produced' gives an index (C/egg) of the energy required to produce one egg (Table 3). The values of 'C/egg' are dependant on female size (Fig. 5). Two methods are now used to study the energy consumption of females:

- method 1: For females of a given size, the regression equation I (Fig. 3) allows the calculation of the energy consumption to produce a given number of eggs. When females produce more eggs (as in nature), we estimate the energy consumption using a simple rule of 3.
- method 2: In nature, we can estimate the number of eggs produced by females using the regression equation I (Fig. 4). The energy consumption is then calculated by referring to the values of 'C/egg' given for the females of the same size (Fig. 5, regression equation II).

Theoretical values of the consumption of females derived by the two methods are similar (Table 4). Hence, the energy required to produce one egg is not influenced by the feeding regime of spiders. The number of eggs per cocoons is dependant on female size and on the quantity of food intake. We use the ratio C/egg to estimate the energy requirements of the adult population in the field.

Energy Requirements in Nature

For individuals of the same juvenile instars, the consumption varies with time of year of the spiders appear (Table 5). Individuals of cohort C2 have, in most instars, an higher consumption than those of cohort C1 although the average size in the two cohorts is similar (Fig. 6). Hence, the spiders of cohort C2 live closer to the thermal preferendum than those of cohort C1.

According to the caloric equivalent of the prey caught in natural areas (22.6 J/mg dry weight), we can estimate the food consumption of the orb-weaving population. In the mesophilous heathland investigated, the total fresh weight of prey consumed by the population in its biological cycle is 0.036 kg/20 m^2 which amounts to 18.2 kg/ha. The amount of food ingested varies with the instar. The high mortality rate (Table 5) reduces total consumption in the first three juvenile instars. In later instars, although the spider density decreases, food intake by the population increased owing to a concommitant increase in individual consumption. The quantity of prey caught by adult females is higher than for the whole juvenile population (Table 6, Fig. 7).

CONCLUSIONS

The species responds to variation of the trophic conditions in both body size and the number of eggs produced. These two biological parameters constitute indices of reference to estimate the quantity of prey caught by the population during the biological cycle. Compared with the results of others (Table 7), the food intake by the population of *Larinioides cornutus* represents from 8.2-36.4% of the total food consumption of the spider communities of different ecosystems. In other respects, the food ingested in the biotope studied

Biotope	Prey killing rate (kg/ha/year)	Country
Reed belt of lake	5-12	Austria
Grassland	52	U.S.A.
Grassland	>150	Switzerland
Grassland	120	Poland
Forest	100	Germany
Spartina swamp	215	U.S.A.

TABLE 7. Prey killing rate by spider communities of vegetation of different ecosystems (after Nyffeler, 1982).

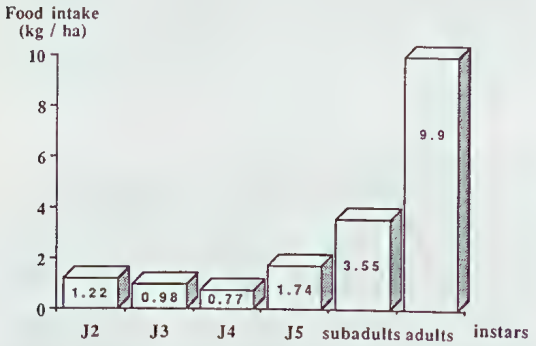

FIG. 7. Food intake by population in biological cycle.

is five times as important as the food ingested by the population studied by Kajak (1967) in a Polish grassland. This is the only analysis of the characteristics of population dynamics of an orb-weaving spider in a temperate region and emphasizes the importance of the secondary productivity.

ACKNOWLEDGEMENTS

I wish to express my most sincere thanks to Dr Y. Lafranche (Institut de Recherche en Mathématiques de Rennes), who greatly contributed in the mathematical treatment of data and helped in the production of the pseudo-cubic spline. I should also like to acknowledge Pascal Dahyot-Cornée who improved the translation.

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STUDIES ON THE WOLF SPIDERS (ARANEAE: LYCOSIDAE). I. A NEW GENUS AND SPECIES FROM KAZAKHSTAN, WITH COMMENTS ON THE LYCOSINAE

ALEXEY A. ZYUZIN

Zyuzin, A.A. 1993 11 11: Studies on the wolf spiders (Araneae: Lycosidae). I. A new genus and new species from Kazakhstan, with comments on the Lycosinae. *Memoirs of the Queensland Museum* **33**(2): 693-700. Brisbane. ISSN 0079-8835.

A new genus *Oculicosa* (Araneae: Lycosidae: Lycosinae) is established and a new species *Oculicosa supermirabilis*, sp. nov. is described from South-western Kazakhstan. Relationships of the new species are analysed. The role of some morphological features of burrowing lycosids is specified. Tegular (median) apophysis in all members of the subfamily Lycosinae is declared to serve as the functional conductor of the embolus: the mechanism of its action is analysed. The role of some structures and the use of corresponding names is specified, the comparison of the main subfamilies is given. The structure of the tribe Trochosini Zyuzin, 1990 is revised: this tribe is divided into two subtribes including non-burrowing and burrowing forms.

On établit un genre nouveau *Oculicosa* (Araneae: Lycosidae: Lycosinae) et décrit une espèce nouvelle *Oculicosa supermirabilis* sp. n. du Sud-Ouest du Kazakhstan. Les affinités de l'espèce nouvelle sont analysées. On précise le rôle des quelques indices morphologiques des Lycosidés creusants. On a déterminé que l' apophyse tegulaire (median) chez tous les membres de la sous-famille Lycosinae sert de conducteur fonctionnel d'embolus: le mécanisme de sont action est analysé. On précise le rôle de quelques structures el l'usage des noms correspondants, la comparaison des principales sous-familles est donnée. On fait une révision de la structure de la tribu Trochosini Zyuzin, 1990: cette tribu se divise en deux sous-tribus insérant des formes non-creusantes et creusantes. □*Lycosidae, Oculicosa, conductor.*

Alexey A. Zyuzin, Institute of Zoology, Kazakhstan National Academy of Sciences, Akademgorodok, 480032 ALMA-ATA 32, Kazakhstan Republic; 18 March, 1993.

Burrowing spiders of the family Lycosidae within Kazakhstan are poorly known. Records exist only for *Allohogna singoriensis* (Laxmann, 1770), *Lycosa nordmanni* (Thorell, 1875) (= *L. narbonensis* auct., non Latreille, 1806), and *L. alticeps* (Kroneberg, 1875) (see Charitonov, 1932; Dubinin, 1946). However, of those, only the distribution in Kazakhstan of *A. singoriensis* has been well studied (see Marikovskij, 1956). The only large non-burrowing lycosid reported from Kazakhstan is *Hogna radiata* (Latreille) (see Schmidt, 1895: Aral Sea and Mangyshlak Plateau). That report is very doubtful, as the author studied juvenile specimens only.

MATERIAL AND METHODS

Spider material I collected in 1989 in Karynzharyk sands, South-western Kazakhstan, are used here. Specimens were captured at night with the use of a miner's head torch: spider's eyes reflect torch light at the distance of 20-25m and even more. Spiders were examined in 70% alcohol using binocular microscopes. To understand the relative position of different parts of the male and female genital apparatus during copulation, dissected tegular apophyses of males were attached to female epigynes (Fig. 5). Eye measurements are given in eyepiece micrometer units (x32). Genitalia and their parts for scanning electron microscopy were preserved in ethanol, air-dried, mounted on stubs, gold-coated and examined in a JEOL JSM-T200 at 15kv.

Abbreviations: ALE, anterior lateral eyes; AME, anterior median eyes; ARE, anterior row of eyes; AZ, private collection of the author; L, leg; LC, carapace length; P, palp; PLE, posterior lateral eyes; PME, posterior median eyes; TA, tegular apophysis; WC, carapace width; ZMMU, Zoological Museum of the Moscow University.

MORPHOLOGY AND DISCUSSION

Oculicosa gen. nov.

TYPE SPECIES

Oculicosa supermirabilis sp. nov.

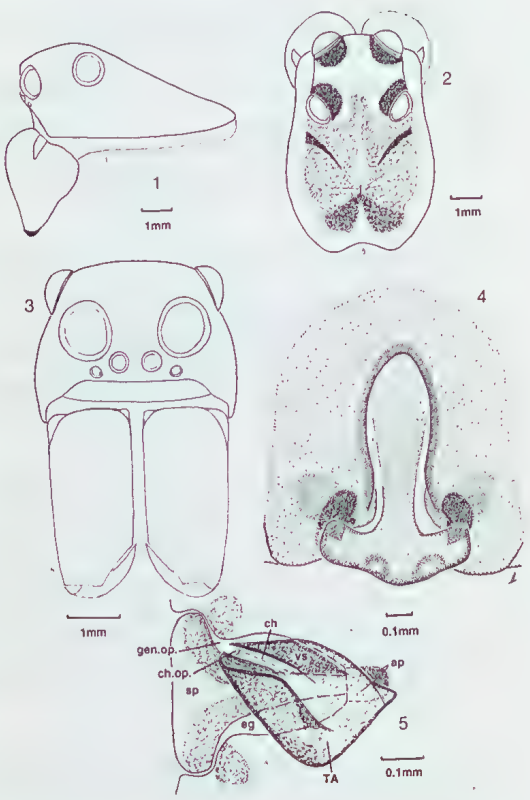
DIAGNOSIS

Medium size (body length 12-20mm). Cephalothorax: head strongly elevated; thorax in both sexes behind ALE is evidently descending

	PME	PLE	AME	ALE
PME	-	0.93-0.98	0.33-0.36	0.23-0.24
PLE	1.02-1.07	-	0.34-0.38	0.23-0.24
AME	2.80-3.00	2.67-2.93	-	0.63-0.71
ALE	4.20-4.42	4.10-4.30	1.40-1.58	-

TABLE 1. Relative size of eyes in *Oculicosa supermirabilis*, sp. nov. (2♂, 2♀)

towards abdomen (Fig. 1), lateral sides of head are almost vertical. Carapace is relatively narrow, ratio LC/WC is 1.44-1.50. PME and PLE are very large, height of ocular field is 0.39-0.42 of LC (Fig. 2). ARE recurved, AME larger than ALE (Fig. 3). Row 1 is 1.64-1.70 times shorter than row 2; row 3 is 1.19-1.23 times wider than row 2. Clypeus narrow, its height less than 1 diameter of AME. Retromargin of cheliceral fang furrow with 2 large equal teeth. Ti + Mt I and II with 2 ventral pairs of spines except apical ones. Base of embolus in lateroapical position, TA is transverse lamella with narrow stout process by its base, directed ventrad, and with sclerotized edge situated distally (Figs 6-8). TA on its inner (dorsal) side with deep narrow transverse sinuous channel opened at the distal end of sclerotized edge. Epigyne has narrow anterior part and widened posterior (genital) parts where transverse genital part of septum is situated (Fig. 4).



FIGS 1-4. *Oculicosa supermirabilis*, sp. nov.: 1, female carapace, lateral view. 2, ditto, dorsal view. 3, ditto, frontal view. 4, epigyne. 5, position of tegular apophysis on epigyne in *Alopecosa cuneata* (Clerck) during copulation. Abbreviations: ap, anterior pocket of epigyne; ch, channel of tegular apophysis; ch. op., channel opening; eg, epigynal groove; gen.op, genital opening of epigyne; gps, genital part of septum; sp, septal pedicle; vs, ventral spur('hook') of tegular apophysis evident through cuticle.

DISTRIBUTION

South-Western Kazakhstan.

Oculicosa supermirabilis sp. n.
(Figs 1-4, 6-8)

MATERIAL EXAMINED

TYPES. Holotype ♂, South-Western Kazakhstan, Mangistau Area, Yeraliev District, 37 km S of Akkuduk Vill., Karynzharyk sands (42°38'N, 54°03'E), clay soil, S.I. Ibraev and A.A. Zyuzin (ZMMU), 14-15 May 1989. Paratypes: 7 ♂, 3 ♀, same data; 1 ♂, 3 ♀, same data, except 15-16 May 1989 (1 ♀ paratype in ZMMU, remainder in AZ).

DESCRIPTION

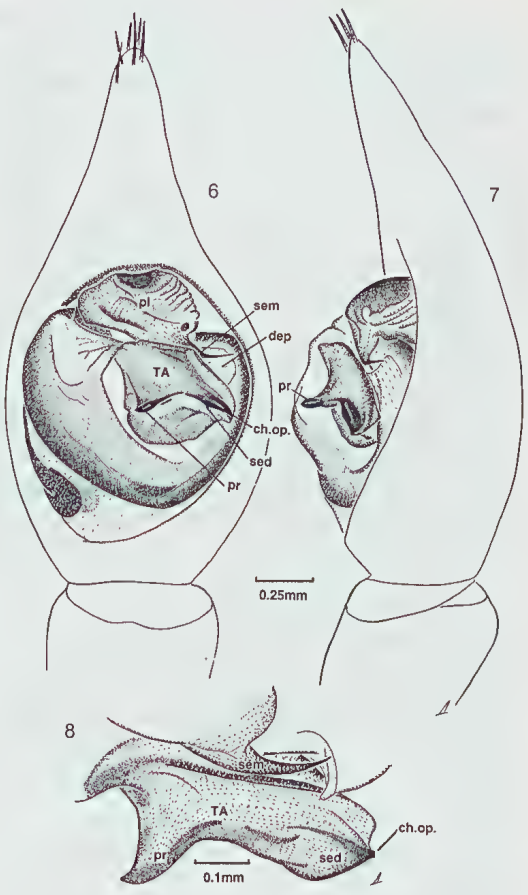
Female. Carapace brown or light brown. Lateral bands wide, continuous, forming wide light 'cheeks' at the sides of head. Median band represented by yellowish rhomboidal spot lying

Female (carapace length = 7.0mm)								Male (carapace length = 7.05 mm)						
Leg	Femur	Patella	Tibia	Met.	Tarsus	Total	T/CL	Femur	Patella	Tibia	Met.	Tarsus	Total	T/CL
1	5.20	2.40	3.70	3.40	1.80	16.50	2.36	6.20	2.70	5.15	5.50	2.50	22.05	3.13
2	5.00	2.15	3.35	3.35	1.80	15.65	2.24	6.10	2.60	4.80	5.60	2.60	21.70	3.08
3	4.60	2.00	3.20	4.00	1.80	15.60	2.23	6.00	2.35	4.60	6.70	2.70	22.35	3.17
4	5.80	2.30	4.30	5.70	2.25	20.35	2.91	7.30	2.50	5.80	8.50	3.25	27.35	3.88
P	2.70	1.50	1.60	-	2.00	7.80	1.12	3.20	1.50	1.60	-	2.10	8.40	1.19

TABLE 2. *Oculicosa supermirabilis*, sp. nov.: length of leg and palp segments in millimetres. T/CL, total leg length/ carapace length; met., metatarsus.

above median furrow (Fig. 2); sometimes this spot is triangular with its base near PLE. Ocular field yellowish-brown, with dark spots around eyes. Carapace evidently descending behind PLE and is supplied with dense fur-like whitish hairs at its edge. Legs: coxae covered dorsally with dense whitish long hairs. Remaining segments uniform yellowish; their length given in Table 2. Leg spination: femora I and II with 2 promesolateral spines; tibiae I and II with 2-2 ventral spines and 2 small apical ones, 1-1 mesolateral, no ectolateral spines; tibiae III and IV with 1-1 dorsal; metatarsi I and II with 2-2 ventral + 4 apical, 1-1 mesolateral, no ectolateral spines; tarsi I-IV dorsally with 2 submedian long setae. Palp: all segments uniform yellowish, but tarsus distally a little darker, tarsal claw long, slightly curved, with 4 very small teeth. Abdomen: sides with dispersed dark points; dorsal pattern consists of brownish lanceolate stripe with dark margins, series of light spots lying below, and whitish spots of different size around. This pattern is covered with dense whitish pubescence. Ventral side above epigastrum dark, with dense dark hairs and bristles, sparse dark hairs are also on spinnerets and at stigmal area, the remainder uniform whitish, but sometimes there are 2 closely situated, almost parallel longitudinal dark lines. Coxae ventrally yellowish-brown, sternum yellowish with some dark hairs on sides, labium and maxillae yellow-brown. Chelicerae reddish-brown, basal segment is covered with long dense whitish-grey hairs and bristles in front. Retromargin of cheliceral fang furrow with 2 teeth, promargin with 3. Body length 15.0-20.2 mm, LC 6.5-8.0 mm. Epigyne: Fig. 4.

Male. Body covered with white hairs. Pattern of both carapace and abdomen as in female, but carapace covered with many whitish-grey adpressed hairs. Ocular field with long and dense whitish hairs. Carapace edged with a narrow stripe of long dense fur-like whitish (silvery) hairs directed anteriad; many short, adpressed silvery hairs also at sides of head and form 'cheeks'. Legs: colouration as in female, coxae dorsally with long and dense silvery hairs. Length of legs as in Table 2. Leg spination: femora I and II as in female; tibiae I-IV with 1-1 dorsal spines, sometimes only prodorsal remains, laterally on each side 1-1, ventrally 2-2 + 2 apical; metatarsi I and II with 1-1 lateral on each side, ventrally 2-2 + 5 apical; tarsi I and II dorsally with 2 submedian long setae. Palp: segments yellow, cymbium distally brownish; all segments covered with white hairs: femur with sparse hairs, patella with many



FIGS 6-8. *Oculicosa supermirabilis*, sp. nov.: 6, male palpus, ventral view. 7, ditto, lateral view. 8, male tegular apophysis with synembolus, apical view. Abbreviations: ch. op., channel opening of tegular apophysis; dep, tegular depression; pl, palea; pr, stout process of tegular apophysis; sed, sclerotized edge of tegular apophysis; sem, synembolus.

short and adpressed hairs, tibia and cymbium (except its distal part) with long and dense hairs. Dentation of cheliceral furrow as in female. Body length 12.0-13.8 mm, LC 6.3-7.3 mm. Palpus: Figs 6, 7.

Ecology

All adults were collected in clayey parts of Karynzharyk sands.

Discussion

Oculicosa supermirabilis is closely related to some species of *Lycosa* s. lat., namely *Lycosa alticeps* (Kroneberg, 1875) and *L. medica* (Pocock, 1889), but differs from them by the

	Lycosinae	Evippinae	Pardosinae	Wadicosinae[1]	Venoninae[2]	Piratinae
1	a2-a3	a2	a2	a2	usually a1	a1-a2
2	b1; seldom b3 [3]	b1	b1	b1	b1-b2	b1; seldom b2 [4]
3	usually c1; seldom c2 & c3	c3	c3	c1	c1	c1; seldom c2 [5]
4	d1; seldom d3	d2	d2	d2	d2	d1-d3
5	e2	e3	e1	e2	e1	e3
6	f1	f1	f1-f2	f1	f1	f3
7	g1	g1	g1	g2	g1	g1
8	h1	h1	h1	h2	h2-h3	h1
9	i2; seldom i3	i3	i1	i4	?	i5
10	j1	j2 [6]; j6 and j2 [7]	j3	j4	j5	j6
11	k1; k5, usually k2; seldom k7 [3]	k2	k1, usually k2	k3	k4	k5-k6; seldom k4

CHARACTERS

1. Size: a1, small; a2, medium; a3, large-very large
2. Carapace, cephalic area: b1, high; b2, narrow; b3, protruding basally with anterior row of eyes
3. Carapace, posterior ocular trapezium: c1, trapezoidal; c2, wide trapezoidal; c3, +/-quadrangular
4. Carapace, size of anterior eyes: d1, variable; d2, small; d3, comparatively large
5. Male palp, origin of embolus: e1, mesolateral; e2, lateroapical; e3, distal (apical)
6. Male palp, shape of embolus: f1, long curved spine; f2, enlarged at tip; f3, short, combined with conductor
7. Male palp, tegulum: g1, no sclerotized processes; g2, with 1-2 stout well sclerotized processes
8. Male palp, tegular (median) apophysis: h1, thick, well sclerotized; h2, weakly sclerotized (membranous); h3, absent
9. Male palp, bed of tip of resting embolus: i1, small tegular depression; i2, enlarged tegular depression; i3, deep dorsal channel of TA; i4, tegular depression on upper tegular process; i5, deep ascending tegular groove
10. Male palp, character of conductor: j1, deep dorsal transverse channel of TA; j2, deep dorsal longitudinal channel of TA; j3, thick well-sclerotized basal part of palea concealed by tegulum; j4, opened (free) transverse sclerotized lateral process of the basal part of palea; j5, opened large apical; j6, combined with embolus (single complex)
11. Epigyne: k1, variable; k2, median inverted T-shaped plate; k3, entire plate with 2 parallel oblong grooves above; k4, simple entire plate; k5, simple hairy plate; k6, hairy plate with lateral sclerites; k7, posteriorly protruding hairy plate

TABLE 3. Comparison of lycosid subfamilies. Notes: [1] *Wadicosa*; [2] after Lehtinen & Hippa, 1979; [3] *Hippasa*; [4] *Aulonia*; [5] *Hygrolycosa*; [6] *Xerolycosa*; [7] *Evippa*.

shape of epigyne and tegular apophysis, by the profile of carapace (cf. Kroneberg, 1875, pl. IV, fig. 28; Pocock, 1889, pl. XIII, fig. 1), as well as by relatively larger PME and PLE, presence of only 2 teeth at the retromargin of chelicerae (in *L. alticeps* and *L. medica* 3), colouration of the ventral side of abdomen and smaller body length.

The descending carapace in both sexes of *Oculicosa supermirabilis*, fur-like hairs at the edges of carapace, and the long and dense whitish hairs on the dorsal side of coxae indicate a burrowing way of life (see also Zyuzin and Zarko, 1989; Zyuzin, 1990), although I could not find the burrows of this species. Our investigations showed that carapace pubescence together with dense hairs on the coxae considerably diminish the friction between the coxae and the edges of carapace; in the much more active males these features are more pronounced and supplemented with many dorsal adpressed whitish-grey hairs on the carapace thus facilitating their movements in burrows. The role of carapace descent is as follows. The comparatively long femora III and IV press against the carapace when moving in narrow burrows: the length of femur IV is slightly longer than the carapace slope. Long-legged males of burrowing lycosids very often have a low flattened carapace (as well as females of the genus *Lycosa* s. str., e.g. *Lycosa tarantula* and *L. nordmanni*: see Zyuzin, 1990): this compensates for the lack of descent, facilitates the folding of very long femora and improves the mobility of these spiders. I suggest that the strongly descending carapace not only in females but also in males (as in *Oculicosa*), together with comparatively narrow carapace, indicates the burrowing way of life from the early juvenile stages up to their imaginal moult: therefore, the distribution of such species is probably very restricted. On the contrary, in *Lycosa nordmanni* and *Allohogna singoriensis* with their flattened carapace in males, mature females seem to be more or less burrowing, while the juveniles, especially early stages, are active. This feature undoubtedly facilitates aerial dispersion of juveniles: as a result, both of these species are widely distributed.

PALPAL MORPHOLOGY

Further discussion concerns the terms 'conductor' and 'terminal apophysis', as their interpretation by different authors is sometimes rather contradictory.

Conductor

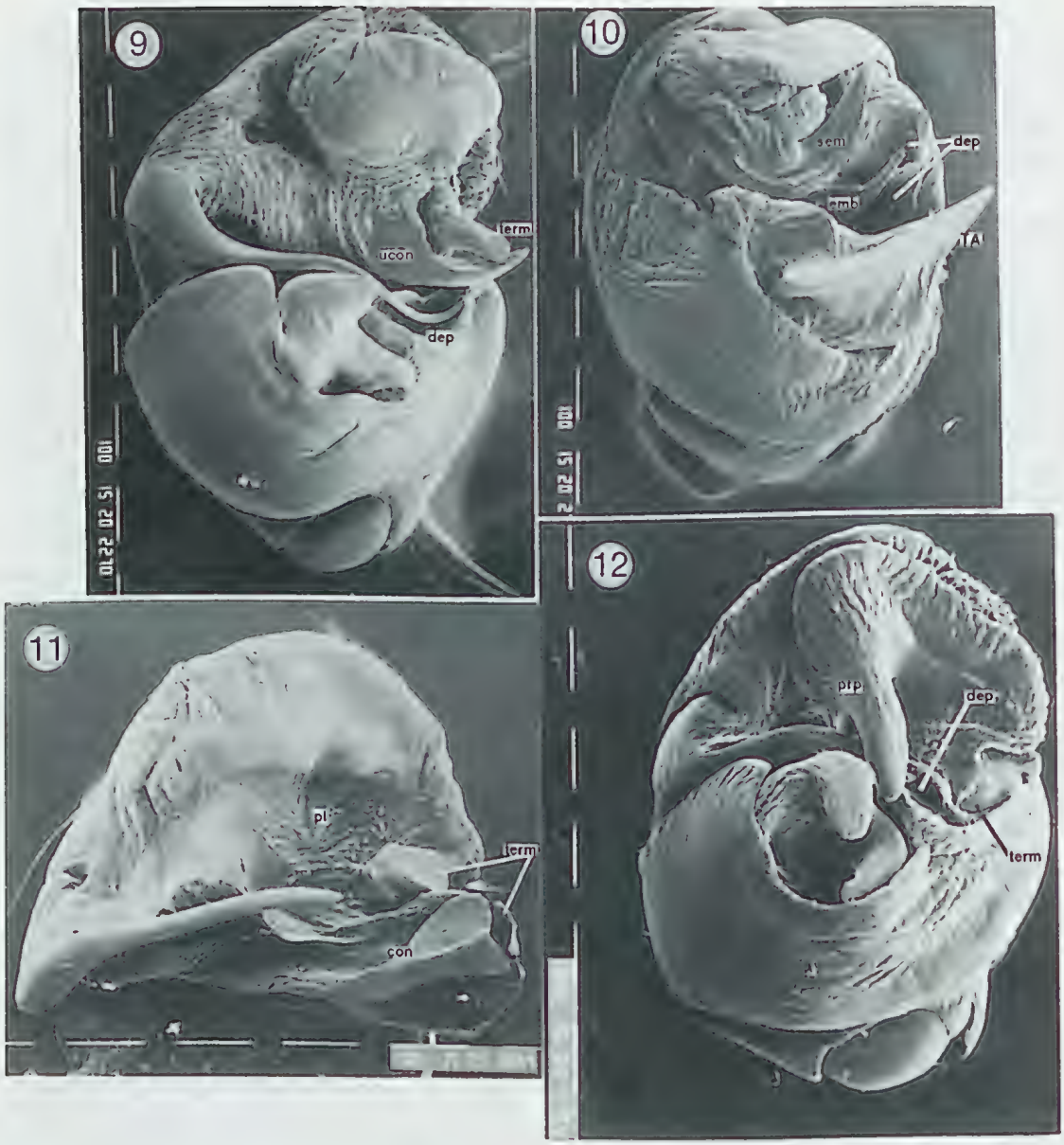
The tip of the resting embolus in both Pardosinae (at least in *Pardosa* and *Acantholycosa*) and Lycosinae lies in the oblong depression of the tegulum: in Pardosinae this depression is rather small and spoonlike (Figs 9, 12), while in Lycosinae it is enlarged, sometimes strongly, and usually forms the tegular lobe (Fig. 10; Dondale, 1986, figs 12, 13). In an unexpanded palp of Pardosinae the depression of the tegulum fully separates the embolus from the true (functional) conductor which is the transverse well-sclerotized groove situated near the base of the terminal part (shield, palea) of the genital bulb and almost fully concealed by the tegulum (Figs 9, 12). In members of Lycosinae, the enlarged depression of the tegulum is regarded as the conductor of the embolus (see Dondale and Redner, 1979; Dondale, 1986), though this bed for the resting embolus does not fit to assist the exact movement of the embolus tip to the female copulatory opening. Lehtinen and Hippa (1979) write: 'We are aware that "conductor" is not a very suitable name for the outer part of the Lycosid embolic division, because it is not always a functional conductor'. Our investigations have shown that the deep transverse channel on the inner (dorsal) surface of tegular apophysis opened at its narrow distal end and diagnostic for all members of the subfamily Lycosinae (Dondale, 1986) is intended for the embolus and undoubtedly directs its tip to the copulatory opening: thus, the TA of Lycosinae serves as the functional conductor. The mechanism of operation of such a conductor during copulation is shown in *Alopecosa cuneata* (Clerck) (Fig. 5): while the hooked ventral spur of the TA comes into contact (forms a hook-up) with the anterior pockets of the epigyne, the ventral rib of the 'hook' enters the longitudinal epigynal groove, so that the channel opening lying at the distal end of TA comes into proximity with the copulatory opening of the epigyne.

Above the embolus and behind the TA in many species of Lycosinae is situated a narrow, sharpened laminar process (see Figs 6-8) usually slightly grooved on its ventral side: the proposed name for this laminar process of palea in Lycosinae is 'synembolus', as it always accompanies the embolus and has the same direction. I suppose that the embolus during copulation enters the TA channel together with the laminar synembolus which directs the embolus to the channel and probably locks the last as a stopper, fully excluding the deviation of the embolus. Thus, the synembolus plays the role of auxiliary conductor. In species of the *Alopecosa pulverulenta* group the synembolus is fused with the base of the palea, so that only an ectal tooth remains at its external side: in this case all the base of the palea goes to the wide 'antechamber' before the channel.

Dondale (1986) correctly regards the subfamily name Hippasinae to be a junior synonym of the Lycosinae. In representatives of the genus *Hippasa* TA also serves as the functional conductor: despite the lack of an atrium in some *Hippasa* species (e.g. *Hippasa deserticola* Simon, and *H. cinerea* Simon) and the agelenid habit of the spiders, I regard them, as well as allied genera, to represent the tribe Hippasini Simon, stat. nov. in the subfamily Lycosinae (see Table 3).

Besides the Lycosinae, the conductor is represented by the tegular apophysis in two other subfamilies: Evippinae (type: *Evippa* Simon) and Allocosinae (type: *Allocosa* Banks).

1. Evippinae. Members of this subfamily have a hooked longitudinal TA which somewhat resembles the transverse trochosoid 'hook' of Lycosinae. As in the species of Lycosinae, the members of Evippinae have a distinct channel on the inner (dorsal) side of TA and a pedicled septum widened posteriad (Zyuzin, 1985, figs 15, 16, 20-22). But, despite these similarities, the genera *Evippa* and *Xerolycosa* have a number of features which allow them to be regarded as members of the separate subfamily. Thus, the channel on the dorsal side of TA in Evippinae is longitudinal (in all Lycosinae it is transverse); the whole embolus is situated in a deep depression and forms a very characteristic recurved flat loop; the base of embolus always has an apical position; the palea is strongly reduced; and the epigynal grooves are very shallow and lie at the level of the septal pedicle. Besides, in *Evippa* spp. the synembolus is transformed into a narrow functional conductor which is constantly situated in a channel of TA and projected beyond the TA limits: in this case TA serves as an auxiliary conductor. In *Xerolycosa* spp. the functional conductor is represented by TA: the embolus constantly lies in a channel (see Zyuzin, 1985); the



FIGS 9-12. Scanning electron micrographs: 9, 10, 12, genital bulbs dissected from cymbia; 11, palea with embolus and conductor dissected from genital bulb). 9, *Pardosa sodalis* Holm. 10, *Hogna radiata* (Latreille). 11, *Pardosa chionophila* L. Koch. 12, *Pardosa turkestanica* (Roewer). Abbreviations: con, conductor; dep, tegular depression; emb, embolus; pl, palea; prp, process of palea; sem, synembolus; TA, tegular apophysis; term, terminal apophysis; ucon, upper branch of conductor. Scale bar=0.1mm.

synembolus is strongly reduced and fused with the semi-transparent extension of the embolus.

2. Allocosinae. In *Allocosa* spp. TA is double-branched, the channel is situated on the dorsal side of the narrow basal branch and holds the tip of the resting embolus; and the atrium of the epigyne is lost (see Dondale and Redner, 1983; Dondale, 1986). Besides, the basal part of the pardosoid palea probably serves as an auxiliary conductor directing the embolus into the channel of TA in the expanded palpus.

In the genus *Pirata* and allied genera (*Piratula, Aulonia, Hygrolycosa*) the functional conductor is combined with a short thin embolus in a com-

mon sickle-shaped complex resting in a deep and narrow ascending tegular groove. The distal position of the well sclerotized conductor in representatives of the subfamily Venoniinae (*Venonia* and allied genera: see Lehtinen and Hippa, 1979) does not allow us to include *Pirata* in the subfamily Venoniinae, as Dondale (1986) did. *Pirata* and allied genera probably deserve to be included in the separate subfamily Piratinae (type: *Pirata* Sundevall, 1832) (see Table 3).

Terminal Apophysis

Very often the palea in Pardosinae (at least in *Pardosa* and *Acantholycosa*) above the embolic division is supplied with a stout, very sclerotized process: many authors (e.g. Holm, 1947; Tongiorgi, 1966; Kronestedt, 1975) designate this process as the terminal apophysis. Dondale (1986) writes '... the terminal apophysis ... is believed to assist the finding and penetration of the copulatory opening by the embolus tip'. It is therefore obvious that, to play this very important role, the terminal apophysis must be situated immediately above the end of the conductor (Figs 9, 11; Kronestedt, 1975, fig. 3); sometimes the dentiform terminal apophysis is situated directly at the outer part of the conductor (see Dondale and Redner, 1984, figs 21, 25, 26). At the same time, there are many cases when the much larger paleal process is situated far above the conductor, i.e. so that it cannot assist the exact penetration of the embolus tip into the female copulatory opening (Fig. 12); however, such a process is also wrongly designated as the terminal apophysis (see Lowrie and Dondale, 1981, fig. 10; Dondale and Redner, 1984, fig. 5; Dondale, 1986, fig. 7). Tongiorgi (1966, fig. 1) correctly designates the true terminal apophysis and the laminar process: the destination of such a process is otherwise, e.g. to protect the resting embolus, or to make an engagement during copulation.

An incorrect designation of terminal apophysis is also used by Buchar (1976, figs 7, 8): in his fig. 8 it is a mere tubercle of the palea, while in fig. 7 (*Pardosa thaleri*) this author confuses it with the narrow laminar conductor sharpened at the tip and characteristic for the *Pardosa bifasciata* group. The similar conductor shape, also designated as the terminal apophysis, is in the species '*Pardosa*' *oncka* Lawrence (see Kronestedt, 1987, fig. 4C).

In some works the synembolus of Lycosinae is also called the terminal apophysis (see Dondale and Redner, 1979, 1990; Dondale, 1986). But, as the synembolus only directs the embolus to the channel of TA (see above), the role of the true terminal apophysis is fulfilled by the ventral process(es) of TA fixing the last on the female epigyne. The designation of the ectal tooth of palea in the *Alopecosa pulverulenta* group as the terminal apophysis (see Kronestedt, 1990) is also incorrect: actually this tooth is the synembolus (see above).

Formerly (see Zyuzin, 1990), I restricted the Lycosini to burrowing lycosids only, and erected the new tribe Trochosini for non-burrowing genera of Lycosinae. Herein the structure of both these tribes is revised: thus, I include in Trochosini only those genera that are characterized by the very peculiar TA which has a transverse lamella with a ventrally directed trochosoid 'hook', or spur, and the epigynal septum with a distinct narrow pedicle, widened posteriad, very often in the shape of an inverted 'T'; epigynal grooves on either side of septal pedicle are rather deep and distinct. Both non-burrowing and burrowing lycosids are included in this very large tribe, undoubtedly having a common origin; in accordance with this view the tribe Trochosini is divided into two subtribes: Trochosina Zyuzin, stat. nov. (including the non-burrowing genera *Trochosa*, *Alopecosa* s. str., *Hogna* s. str., *Schizocosa*), and Geolycosina, subtrib. nov. (including the burrowing genera *Arctosa* s. str., *Geolycosa*, *Allohogna* with a very characteristic carapace profiles: see Zyuzin, 1990, fig. 1). There are many species throughout the world, including African ones, which also belong to the Trochosini: the generic and subtribal position of these remain obscure due to the artificial system of Roewer (1959-1960).

As shown in Fig. 5, the length of the epigynal groove and septal pedicle in species of Trochosini is correlated with the length of the ventral spur of TA.

As to the tribe Lycosini, I place here only the members of *Lycosa* s. str. with their very peculiar genitalia, and some allied species referred to *'Allocosa'*, *'Hogna'* and probably *Metatrochosina* (Roewer, 1959-1960, figs 124, 126, 129, 219, 304-305, 517).

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